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VOL. 11, NO. 1 MAY 1942

# STUDIES ON THE BIOLOGY OF THE LARVA OF THE NEMATODE LUNGWORM, *MUELLERIUS CAPILLARIS*, IN MOLLUSCS

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## 1. INTRODUCTION

UNTIL 1929 it was thought that the life history of *Muellerius capillaris* (Müller, 1889), a nematode lungworm of sheep and goats, was a direct one, but in that year Hobmaier & Hobmaier (1929) demonstrated that a large number of molluscs serve as potential intermediate hosts for *Muellerius*, and that in the absence of these hosts, the worm is unable to complete its life history. Through this and subsequent work (1930) they were able to cite the following molluscs as intermediate hosts of *M. capillaris*. (I have added the authors' names together with any necessary comment.)

Agriolimax agrestis (Linn.)
A. reticulatus Müller
Arion subfuscus (Draparnaud)
A. hortensis Férussac
A. circumscriptus Johnston
A. empiricorum Férussac [=A. ater (Linn.)]
Fruticicola hispida Linn.
Monacha umbrosa Partsch
M. bidens (I am unable to trace this mollusc)
Cepaea hortensis (Müller)
Helix pomatia Linn.
Cingulifera planospira Lam.
Arianta arbustorum (Linn.)
Limax cinereus Müller [=L. maximus Linn.]
L. flavus Linn.
Succinea putris (Linn.)
S. pfeifferi Rossmässler

Briefly, the life cycle of *Muellerius capillaris* as described by Hobmaier & Hobmaier is as follows. The eggs usually hatch in the lungs of the hosts, and the larvae are coughed up. These larvae remain in the ground until they come in contact with a suitable mollusc. When this happens the larvae enter the mollusc, usually by burrowing into the foot. In the foot of the mollusc the larvae moult twice, retaining the two moulted skins, so that the infective larva is enclosed in the loose sheaths of the first- and second-stage larvae. The infective stage is reached in about 12 days from the entry of the free-living larvae into the mollusc. These infective larvae will not develop further unless the mollusc is ingested by a sheep or goat. In the sheep or goat the larvae continue their development until the adult form is reached.

The biology of the free-living stage has been worked out fairly completely (Morgan, 1929; Hobmaier & Hobmaier, 1929, 1930), and is not discussed to any length in this paper, other than that part relating to desiccation.

## 2. Material and methods

Sheep lungs showing infection in the form of translucent tumours, each about $\frac{1}{2}$ in. in diameter, were used for obtaining the free-living larvae. The tumours were teased out in tap water, the larger portions removed and the liquid containing the eggs was allowed to stand for about 24 hr. Numerous larvae were then found to be present. Molluscs were obtained from gardens when they were required for experimental purposes, and from fields where sheep grazed when the routine examinations were being made. Artificial infection of molluscs was accomplished by dropping the free-living larvae on the foot or by causing the molluscs to crawl on blotting paper on which the larvae had been placed. The molluscs were killed by drowning. This resulted in their dying in an expanded condition. The foot was then examined in portions squeezed between two slides.

## 3. Resistance of the free-living stage to desiccation

Morgan (1929) states that the free-living larvae of *M. capillaris* can withstand desiccation for periods up to a week, whereas Hobmaier & Hobmaier (1930) state that the larvae are very sensitive to desiccation and that they are killed in a few hours. In the present work it was found that if the free-living larvae were placed on a glass slide and were allowed to dry, the addition of water after a week revived more than half of them. It was also found, as Morgan (1929) stated, that alternation of desiccation and rewetting kills the larvae in 3–4 days.

## 4. Two new intermediate hosts

After a number of artificial infections had been carried out using the recognized intermediate hosts of *M. capillaris*, it was decided to attempt the infection of molluscs which had not hitherto been recorded as intermediate hosts. The little snail, *Hyalinia cellaria* (Müller), is a fairly common mollusc in the Cardiff district, being recorded by Dean (1927) as 'generally distributed'. A number of these snails were obtained from gardens, and half of them were examined and found to be free from any kind of nematode infection. The remainder were placed on damp blotting paper to which free-living *Muellerius capillaris* larvae had been added. Examination of the snails later showed them to be infected. It was found that the first moult occurred after about 8 days, and the second moult after a further 6 days. These times correspond with those given by Hobmaier & Hobmaier (1929) for the other intermediate hosts.

Artificial infection was attempted with *Milax sowerbyi* (Férussac). This slug is frequently found in Cardiff, according to Dean (1927). As in the case of *Hyalinia cellaria*, a number were examined and a further lot from the same

collection was artificially infected. This species also took the infection easily, and here again the times were about 8 days to the first moult and a further 6 days to the second moult.

There appeared to be no resistance on the part of the mollusc to the larvae in either case.

### 5. THE CONDITION OF THE LARVAE IN *ARION ATER*

Hobmaier & Hobmaier (1929) cite *Arion empiricorum* (=*A. ater*) as an intermediate host of *Muellerius capillaris*. *Arion ater* is the common large black slug of this country, and because of its ubiquity and the fact that it is found when other molluscs are in hiding, it was decided to investigate thoroughly its importance in lungworm transmission. Besides the specimens collected during routine investigations, some were gathered from gardens, etc., and artificial infections were attempted. The artificially infected forms, and some of those gathered from pasturelands, were found to contain *Muellerius capillaris* larvae, though in both cases these were in such a condition as to indicate that they could not reach the infective stage.

Hobmaier & Hobmaier (1929) outline two methods of defence on the parts of the various molluscs against the attacks of the larvae. These are, first, the formation of a translucent tubercle around the larva, and secondly, in the case of molluscs which possess yellow mucus or yellow pigment, the deposition of a yellow-pigmented material around the larva. They state that the translucent tubercle becomes loose as the larva grows, and where the yellow-pigmented material is deposited, this usually disappears except for a trace around the head end. This sometimes causes a little trouble during ecdysis. During the present investigation, it was noticed that both methods of defence were used by *Arion ater* against the larvae, and that these methods appeared to be successful. The larvae found were heavily encrusted with a hard yellow material, and surrounded by a translucent tubercle about 0·18 mm. in diameter. This yellow encrustation was quite hard and brittle and remained, when broken, as a number of separate pieces in the vicinity of the larva. The parasite's cuticular spine could now be clearly seen at the base of the undulating appendix. The larvae found were small, about 0·3 mm. long. This is the normal length of the free-living stage. No infective larvae were found at all, and very few of the larvae found appeared to have advanced in structure beyond that of the free-living stage.

Besides the specimens of *A. ater* which were artificially infected, fifty were gathered during the series of collections made from pasture lands. Twenty-three of these slugs were infected. All of the 124 larvae which were found were encrusted with a hard yellow material, and each was surrounded by a translucent cyst.

The conclusion was reached that *A. ater* can be infected with the larvae of *Muellerius capillaris*, but that these larvae do not develop to the infective

stage. *Arion ater* may thus be considered unimportant in the transmission of lungworm disease. The white variety of *A. ater*—var. *albida*—was found once, and it also contained *Muellerius capillaris* larvae in the same condition as those found in the ordinary black variety.

### 6. Natural infections in molluscan hosts

To study the natural infections of molluscan hosts with *M. capillaris*, collections of molluscs were made from various districts where sheep were grazing or where sheep had recently grazed. The collections were made at various times, and in each case the following particulars were recorded: (1) Date of collection, (2) Time of day, (3) Meteorological conditions, (4) Geographical conditions, (5) Condition of ground—wet or dry, etc., (6) *p*H of the soil, (7) Position of the molluscs—free in the grass or under stones, etc.

The observations made on the habits of the molluscs in the various districts were hampered to some extent by the abnormal climatic conditions which existed throughout the year. For instance, during January and February of 1938 the number of molluscs collected was extremely small owing to the dryness of the weather, only three collections yielding appreciable results.

It was noticed that the majority of molluscs collected were rarely found free in the grass during the day unless the ground was wet. Boycott (1934) states that snails and slugs move about either at night when the humidity is high or in wet weather. This is because the loss of water from the skin of the mollusc varies with the percentage humidity of the air. 'When it is dry', he says, 'they retire into the surface of the ground or any other small unventilated space where further water loss is minimised.' Thus it was usually found necessary to look under stones to obtain molluscs during the daytime unless the ground was wet. After rain the molluscs came out, but during the actual time of raining they were found usually only under stones. At night (collections were then made by torchlight) molluscs were found easily, being mostly free in the grass. In the early morning also they were frequently found free in the grass especially when there was a heavy dew. The results of the various collections which were made can be summarized thus. During the night the molluscs were found free in the grass unless there was very heavy rain or a severe drought. During the day the molluscs usually sought the shelter of stones, etc., unless the ground was wet following a heavy dew or a period of rain. Certain exceptions occurred. Such an exception was the prevalence of *Arion ater*, the black slug, which appeared very often when no other slugs could be found free in the grass.

The importance of the habits of the molluscs is obvious in any consideration of the epidemiology of infection with *Muellerius capillaris*, and it is an

interesting fact that the habits of the sheep and molluscs do not 'fit' nearly as well as the habits of many hosts do with those of their respective parasites. During the night, when molluscs are usually free in the pastures, sheep are usually less active, and during the day when they are grazing, the molluscs are sheltering. It appears then that the only time for the transmission of the lungworm larvae to sheep in any appreciable numbers is during the early morning when there is a heavy dew or during the period following heavy rain when the ground is still wet. An evening dew which brings out the molluscs before the sheep have completed grazing is also conducive to the spread of the disease.

Mollusc collections were made from and conditions studied in twelve small areas mainly around Cardiff and in the Rhondda Valley. Two tables are included to indicate the results that were obtained. Table 1 gives details of one area to which particular attention was paid, and Table 2 a tabulation of collected results of all the visits to all the areas. Any significant observation concerning any particular area is included in the general discussion of results.

Table 1. *Locality:* grass bank, Dinas (Rhondda). *Geological formation:* coal outcrops—Pennant Grit. *Height above sea-level:* 500 ft. *Number of collections made:* 13.

| | | | | Position of larvae | | | Stages of larvae | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | No. found | No. infected | No. of larvae | Anterior | Middle | Posterior | 1st | 2nd | Infective |
| *Agriolimax agrestis* | 215 | 38 | 234 | 131 | 73 | 30 | 25 | 8 | 201 |
| *Arion hortensis* | 17 | 3 | 10 | 7 | 3 | 0 | 0 | 0 | 10 |
| *A. subfuscus* | 28 | 5 | 15 | 9 | 3 | 3 | 3 | 1 | 11 |
| *A. circumscriptus* | 13 | 2 | 3 | 2 | 1 | 0 | 0 | 0 | 3 |
| *A. ater* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Limax maximus* | 2 | 2 | 17 | 10 | 6 | 1 | 0 | 11 | 6 |
| *Hyalinia cellaria* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Total | 277 | 50 | 279 | 159 | 86 | 34 | 28 | 20 | 231 |

Total percentage infection = 18·05.

Table 2. *Summary of all collections, Cardiff area and Rhondda Valley (includes data in Table* 1)

| | | | | | Stages of larvae | | |
|---|---|---|---|---|---|---|---|
| Species found | No. found | No. infected | % infected | No. of larvae | 1st | 2nd | Infective |
| *Agriolimax agrestis* | 656 | 94 | 14·17 | 367 | 60 | 17 | 290 |
| *Arion hortensis* | 38 | 5 | 13·16 | 13 | 0 | 0 | 13 |
| *A. subfuscus* | 90 | 18 | 20·0 | 63 | 6 | 1 | 56 |
| *A. circumscriptus* | 41 | 6 | 14·63 | 12 | 0 | 0 | 12 |
| *A. ater* | 50 | 23 | 46·0 | 124 | | Encrusted | |
| *A. intermedius* | 2 | 0 | — | 0 | 0 | 0 | 0 |
| *Limax maximus* | 3 | 3 | 100·0 | 24 | 0 | 11 | 13 |
| *Milax sowerbyi* | 14 | 0 | — | 0 | 0 | 0 | 0 |
| *Hyalinia cellaria* | 4 | 0 | — | 0 | 0 | 0 | 0 |
| Total | 898 | 149 | 16·59 | 603 | 66 | 29 | 384 |

Table 3. *Localities where collections were made*

| Locality | Ht. above sea-level ft. | Months 1938 | Notes |
|---|---|---|---|
| 1. Dinas (Rhondda) | 500 | Feb.–Aug. | Grass bank 100 yd. long, 60 ft. high |
| 2. Penrhiwfer (nr. Tonyrefail) | 600 | May–July | |
| 3. Glyn Valley (nr. Tonyrefail) | 700 | April–May | |
| 4. Penygraig (Rhondda) | 700–1300 | April and July | |
| 5. Llwynypia (Rhondda) | 600–800 | April, May and July | |
| 6. Fields off Newport Road, Cardiff | *c.* 25 | Jan., March and Aug. | |
| 7. Tonyrefail (A) | 650 | April–June | |
| 8. Dinas (Rhondda) | 600–1032 | Jan., April and July | Mountain |
| 9. Taff's Well | 300–400 | April, May and July | |
| 10. Merthyr | 850 | April, July and Aug. | Field on mountain-side |
| 11. Radyr | 300 | April–June | |
| 12. Tonyrefail (B) | 600 | March | About 1 mile from Tonyrefail (A) |

## 7. Discussion

The results of the collections showed that all of the twelve districts contained infected molluscs. *Agriolimax agrestis* is by far the commonest mollusc found in the district around Cardiff and the Rhondda Valley. Also it is the most important in the transmission of *Muellerius capillaris* larvae.

A study of the percentage infections of *Agriolimax* and the *Arion* species, excluding *A. ater*, will show that there appears to be no particular choice of a mollusc by a larva. The relative importance of the various molluscs in the epidemiology of *Muellerius capillaris* disease in any district therefore probably depends on their relative numbers in that district.

The geological formation of the district and the *p*H of the soil do not seem to influence the incidence of either the molluscs or the free-living larvae, as far as these collections show. However, the series of districts studied presented a fair uniformity, and it is possible that in other geological districts the factors mentioned might be found to influence the distribution of either the free-living larvae or the mollusc.

The height above sea-level also does not appear to influence directly the free-living stage of the parasite, but there does seem to be a relation between the various levels of the same district and the molluscs found at each. This was observed in a study of the mountain districts, where it was found that the majority of the molluscs occur at the lower levels, and even the hardy *Arion ater* becomes scarce and ultimately disappears as the higher levels are reached. It seems from this that sheep grazing at the tops of the mountains will be free from the lungworm disease. It was noticed that sheep did graze on the mountain tops but did not confine themselves to this area.

The study of the distribution of the larvae in the mollusc shows that the majority are to be found in the anterior part of the foot, and the least in the posterior part. About 57% of the larvae were found in the fore part, 31% in the middle region, and 12% in the hinder part of the foot. These figures

are based on an examination of 279 larvae in fifty infected molluscs in the No. 1 locality (Table 1), and they confirm the statement made by Hobmaier & Hobmaier (1929) regarding the distribution of the larvae.

There would appear to be a definite correlation between the size of a mollusc and its chance of infection, due, no doubt, to the greater area of the foot, the more rapid rate of movement and, consequently, to the larger area of ground covered. In the following table the species of molluscs are arranged in order of size and this corresponds to their order of percentage infection, the smaller species being relatively less highly infected:

| Species | Size (cm.) | % infection |
|---|---|---|
| *Arion ater* | 15–20 | 46·00 |
| *A. subfuscus* | 6–8 | 20·00 |
| *A. circumscriptus* | 3 | 14·63 |
| *Agriolimax agrestis* | 3 | 14·17 |
| *Arion hortensis* | 3 | 13·16 |

The same point emerges in considering the percentage infection of individuals of a single species arranged in size groups, as the following table of measurements of 410 specimens of *Agriolimax agrestis* suggests:

| Size (cm.) | No. examined | No. infected | % infection |
|---|---|---|---|
| 1·5–2·0 | 140 | 2 | 1·43 |
| 2·0–3·0 | 188 | 32 | 17·00 |
| >3·0 | 82 | 22 | 26·80 |

## 8. SUMMARY

1. The life history of the larva of the sheep lungworm, *Muellerius capillaris*, in the various molluscs, and the description of the various stages as outlined by Hobmaier & Hobmaier (1929, 1930) have been verified.

2. The free-living larvae are resistant to desiccation up to a period of 1 week, and it is thus not essential for them to fall on wet ground to survive.

3. To the list of molluscs given by Hobmaier & Hobmaier (1929, 1930), which serve as intermediate hosts of *Muellerius capillaris*, are added the slug *Milax sowerbyi* and the snail *Hyalinia cellaria*.

4. *Arion ater* plays no part in the transmission of this lungworm.

5. Each of the twelve localities studied in the Cardiff area and Rhondda Valley contained infected molluscs.

6. The free-living larvae of *Muellerius capillaris* do not appear to show any preference for any particular one of the proved intermediate hosts, and the importance of the various molluscs in different districts is directly proportional to the numbers of each present in these districts. In the Cardiff district *Agriolimax agrestis* is the commonest mollusc.

7. At the summits of the mountain districts no molluscs were found and it can be assumed that sheep grazing at these areas would be safe from lungworm disease.

9. Acknowledgements

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# ECOLOGICAL FEATURES OF THE BIRD FAUNAS OF BRITISH SMALL ISLANDS

By DAVID LACK

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## INTRODUCTION

The basis of the present paper was a study of the breeding birds of the Orkney Islands in 1941, the details of which, being primarily of local interest, are published in a faunistic paper elsewhere (Lack, 1942). The present paper is concerned with features of the Orkney bird fauna of more general interest in the study of animal populations, while in addition the literature of bird faunas on other small islands was summarized in order to find which of these features were applicable to small islands in general.

The full data on which Part 1 of this paper is based, a brief description of the Orkneys, a full bibliography of Orkney breeding birds and full acknowledgements are given in the faunistic paper referred to. Here I would particularly acknowledge assistance on the literature of small islands from Miss E. V. Baxter and Miss L. J. Rintoul, and from W. B. Alexander of the Edward Grey Institute of Field Ornithology; and the two former, and J. Fisher and L. S. V. Venables, for contributing previously unpublished information on particular islands.

The breeding birds of Orkney are summarized in Tables 1 and 2. In this study it is necessary to separate the land and fresh-water species from sea and shore birds, and Table 1 shows where this admittedly somewhat arbitrary line is drawn. The order of species in Table 1 is followed throughout the paper. For nomenclature, Witherby and others (1938–41) are followed.

## Table 1. *Breeding birds of Orkney, Shetland and Faeroes*

O indicates regular, o occasional, in Orkney; S and s the same for Shetland, F and f the same for Faeroes. Brackets indicate species now extinct.

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | A. *Land and fresh-water species* | | | | | | |
| Raven (*Corvus corax*) | O | S | F | Peregrine falcon (*Falco peregrinus*) | O | S | |
| Hooded crow (*C. cornix*) | O | S | F | Merlin (*F. columbarius*) | O | S | F |
| Rook (*C. frugilegus*) | O | | | Kestrel (*F. tinnunculus*) | O | S | |
| Jackdaw (*C. monedula*) | O | | | Hen harrier (*Circus cyaneus*) | O | (S) | |
| Starling (*Sturnus vulgaris*) | O | S | F | Sparrowhawk (*Accipiter nisus*) | O | | |
| Greenfinch (*Chloris chloris*) | O | | | Heron (*Ardea cinerea*) | O | | |
| Twite (*Carduelis flavirostris*) | O | S | | Mute swan (*Cygnus olor*) | O | | |
| Linnet (*C. cannabina*) | O | | | Mallard (*Anas platyrhyncha*) | O | S | F |
| Chaffinch (*Fringilla coelebs*) | O | s | | Teal (*A. crecca*) | O | S | f |
| Corn bunting (*Emberiza calandra*) | O | S | | Wigeon (*A. penelope*) | O | S | |
| Yellow-hammer (*E. citrinella*) | O | | | Pintail (*A. acuta*) | O | S | F |
| Reed bunting (*E. schoeniclus*) | O | | | Shoveler (*Spatula clypeata*) | O | | |
| Snow bunting (*Plectrophenax nivalis*) | | s | F | Pochard (*Aythya ferina*) | O | | |
| Tree sparrow (*Passer montanus*) | | s | (F) | Tufted duck (*A. fuligula*) | O | | f |
| House sparrow (*P. domesticus*) | O | S | | Common scoter (*Melanitta nigra*) | O | S | |
| Skylark (*Alauda arvensis*) | O | S | f | Little grebe (*Podiceps ruficollis*) | O | | |
| Meadow pipit (*Anthus pratensis*) | O | S | F | Red-throated diver (*Colymbus stellatus*) | O | S | F |
| Pied/White wagtail (*Motacilla alba*) | O | s | f | Ring dove (*Columba palumbus*) | O | | |
| Willow warbler (*Phylloscopus trochilus*) | O | s | | Rock dove (*C. livia*) | O | S | F |
| Sedge warbler (*Acrocephalus schoenobaenus*) | O | | | Curlew (*Numenius arquata*) | O | S | |
| Mistle thrush (*Turdus viscivorus*) | O | | | Whimbrel (*N. phaeopus*) | (O) | S | F |
| Song thrush (*T. ericetorum*) | O | S | | Snipe (*Capella gallinago*) | O | S | F |
| Redwing (*T. musicus*) | | s | F | Red-necked phalarope (*Phalaropus lobatus*) | O | S | f |
| Blackbird (*T. merula*) | O | S | | Dunlin (*Calidris alpina*) | O | S | F |
| Wheatear (*Oenanthe oenanthe*) | O | S | F | Common sandpiper (*Actitis hypoleuca*) | O | S | |
| Whinchat (*Saxicola rubetra*) | O | | | Redshank (*Tringa totanus*) | O | S | |
| Stonechat (*S. torquata*) | O | | | Golden plover (*Charadrius hiaticula*) | O | S | F |
| Robin (*Erithacus rubecula*) | O | | | Lapwing (*Vanellus vanellus*) | O | S | f |
| Dunnock (*Prunella modularis*) | O | | | Black-headed gull (*Larus ridibundus*) | O | S | F |
| Wren (*Troglodytes troglodytes*) | O | S | F | Corncrake (*Crex crex*) | O | S | F |
| Dipper (*Cinclus cinclus*) | O | | | Water rail (*Rallus aquaticus*) | O | | |
| Swallow (*Hirundo rustica*) | O | s | f | Moorhen (*Gallinula chloropus*) | O | S | |
| House martin (*Delichon urbica*) | O | s | | Coot (*Fulica atra*) | O | S | |
| Sand martin (*Riparia riparia*) | (O) | s | | Red grouse (*Lagopus scoticus*) | O | | |
| Cuckoo (*Cuculus canorus*) | O | s | | Pheasant (*Phasianus colchicus*) | O | | |
| Long-eared owl (*Asio otus*) | O | | | Quail (*Coturnix coturnix*) | o | s | f |
| Short-eared owl (*A. flammea*) | O | s | | | | | |
| | B. *Sea and shore species* | | | | | | |
| Rock pipit (*Anthus spinoletta*) | O | S | F | Common tern (*S. hirundo*) | O | S | |
| Shelduck (*Tadorna tadorna*) | O | S | | Arctic tern (*S. macrura*) | O | S | F |
| Eider (*Somateria mollissima*) | O | S | F | Common gull (*Larus canus*) | O | S | F |
| Red-breasted merganser (*Mergus serrator*) | O | S | F | Herring gull (*L. argentatus*) | O | S | F |
| Cormorant (*Phalacrocorax carbo*) | O | S | F | Lesser black-backed gull (*L. fuscus*) | O | S | F |
| Shag (*P. aristotelis*) | O | S | F | Great black-backed gull (*L. marinus*) | O | S | F |
| Gannet (*Sula bassana*) | | S | F | Kittiwake (*Rissa tridactyla*) | O | S | F |
| Storm petrel (*Hydrobates pelagicus*) | O | S | F | Great skua (*Stercorarius skua*) | O | S | F |
| Fork-tailed petrel (*Oceanodroma leucorrhoa*) | | | F | Arctic skua (*S. parasiticus*) | O | S | F |
| Manx shearwater (*Puffinus puffinus*) | O | S | F | Razorbill (*Alca torda*) | O | S | F |
| Fulmar petrel (*Fulmarus glacialis*) | O | S | F | Guillemot (*Uria aalge*) | O | S | F |
| Ringed plover (*Charadrius hiaticula*) | O | S | F | Black guillemot (*U. grylle*) | O | S | F |
| Oystercatcher (*Haematopus ostralegus*) | O | S | F | Puffin (*Fratercula arctica*) | O | S | F |
| Sandwich tern (*Sterna sandvicensis*) | O | s | | | | | |

*Note.* This table is complete as regards known regular breeding species, but rare and doubtful species are omitted if not regular in any of the three regions. (They are given later.)

Table 2. *Extinct, irregular and doubtful Orkney breeding birds*

A. *Formerly regular, now extinct*

Sand martin (*Riparia riparia*)
Golden eagle (*Aquila chrysaëtus*)
White-tailed eagle (*Haliæëtus albicilla*)
Whooper swan (*Cygnus cygnus*)
Whimbrel (*Numenius phaeopus*)
Ptarmigan (*Lagopus mutus*)

B. *Irregular, but have bred more than once*

Grey wagtail (*Motacilla cinerea*)
Spotted flycatcher (*Muscicapa striata*)
Blackcap (*Sylvia atricapilla*) (probably, not proved)
Whitethroat (*S. communis*)
Ring ousel (*Turdus torquatus*)
Long-tailed duck (*Clangula hyemalis*)
Woodcock (*Scolopax rusticola*)
Quail (*Coturnix coturnix*)

C. *Doubtful breeders, most recorded once only*

(1) *Inland species*

Lesser redpoll (*Carduelis flammea*)
Yellow wagtail (*Motacilla flava*)
Pied flycatcher (*Muscicapa hypoleuca*)
Goldcrest (*Regulus regulus*)
Redwing (*Turdus musicus*)
Scaup (*Aythya marila*)
Velvet scoter (*Melanitta fusca*)
Black-throated diver (*Colymbus arcticus*)
Dotterell (*Eudromias morinellus*)

(2) *Sea birds*

Gannet (*Sula bassana*)
Little tern (*Sterna albifrons*)
Great auk (*Alca impennis*)

*Note.* A few other species have also been recorded doubtfully.

## PART 1. THE ORKNEY BIRD FAUNA

### (*a*) Comparison of Orkney with neighbouring regions

#### *Caithness*

In Caithness, the region of the mainland of Scotland closest to Orkney, 106 species of birds breed regularly (see list in Lack (1942) based on Baxter & Rintoul (1928, 1931 and *in litt.*)). Of these, 17 are sea-birds and all of these breed in Orkney. Of the 89 land and fresh-water species, as many as 25 (28 %) are not established in Orkney. These are:

(1) *Woodland, bush and garden species:* 15. Siskin (*Carduelis spinus*), lesser redpoll (*C. flammea*), bullfinch (*Pyrrhula pyrrhula*), tree creeper (*Certhia familiaris*), great tit (*Parus major*), blue tit (*P. caeruleus*), coal tit (*P. ater*), long-tailed tit (*Aegithalos caudatus*), goldcrest (*Regulus regulus*), spotted flycatcher (*Muscicapa striata*), whitethroat (*Sylvia communis*), redstart (*Phoenicurus phoenicurus*), tawny owl (*Strix aluco*), woodcock (*Scolopax rusticola*), blackcock (*Lyrurus tetrix*).

(2) *Other species:* 10. Grey wagtail (*Motacilla cinerea*), ring ousel (*Turdus torquatus*), sand martin (*Riparia riparia*), swift (*Apus apus*), golden eagle (*Aquila chrysaëtus*), grey lag goose (*Anser anser*), black-throated diver (*Colymbus arcticus*), greenshank (*Tringa nebularia*), ptarmigan (*Lagopus mutus*), common partridge (*Perdix perdix*).

Of these species three (sand martin, golden eagle and ptarmigan) were formerly regular but are now extinct in Orkney. Doubtless this also applies to the grey lag goose, though there are no known Orkney breeding records. Most of the rest are more southerly species which reach in Caithness the northerly limit of their breeding range in Britain. Fifteen of these are

woodland, bush and garden species. Species of this type have been gradually colonizing Orkney since the planting of trees and bushes in the nineteenth century; but, as this list shows, the process is nowhere near completion. Indeed, a number of woodland birds, e.g. lesser redpoll and the four species of tits, are only recent colonists in Caithness. As can be seen from Table 2, some of these Caithness species have bred in Orkney occasionally, without as yet becoming established.

*Shetland*

Orkney, only 6–8 miles from the mainland, has an impoverished bird fauna compared with the mainland. Shetland, 50 miles north of Orkney, shows further considerable impoverishment, as is apparent from Table 1. Of the 25 Orkney sea birds only one, the Sandwich tern, is not established in Shetland. But of the 67 inland species 33 (49 %) are not established in Shetland. These are:

(1) *Woodland, bush and garden species:* 14. Rook, greenfinch, linnet, chaffinch, yellowhammer, willow warbler, mistle thrush, whinchat, robin, dunnock, long-eared owl, sparrowhawk, ring dove, pheasant.

(2) *Other species:* 19. Jackdaw, reed bunting, pied wagtail, sedge warbler, stonechat, dipper, swallow, house martin, cuckoo, short-eared owl, hen harrier, heron, mute swan, shoveler, pochard, tufted duck, little grebe, water rail, red grouse.

Of these 33 species, the 14 woodland, bush and garden species could hardly be expected to breed regularly in Shetland, where there are no woods and few gardens, though a number of them have bred occasionally. Also 19 of these 33 species colonized Orkney only after 1800 (see later), and some of these will doubtless spread to Shetland eventually. One species, the hen harrier, formerly bred but is now extinct in Shetland. The red grouse is not native to Shetland, but has been introduced there.

*Faeroes*

Salomonsen (1935) lists the breeding species of the Faeroes, which lie 170 miles from Shetland. Only two species of sea birds, shelduck and common tern, breed regularly in Shetland but not in the Faeroes. But the land and fresh-water species continue the reduction shown by Shetland as compared with Orkney. The Faeroes are rather deficient in inland waters, and some of the ducks would otherwise doubtless breed there, as they breed farther north, in Iceland. Hence it is more profitable to list those Shetland species which do not breed in either Faeroes or Iceland. These are 13 out of the 35 regular Shetland breeding species (37 %):

(1) *Garden species:* 2. Song thrush, blackbird.

(2) *Other species:* 11. Twite, corn bunting, house sparrow, skylark, peregrine, kestrel, curlew, common sandpiper, lapwing, moorhen, coot.

These tables illustrate the progressive impoverishment of the bird fauna as regards land and fresh-water species the farther that one gets from the mainland: the figures being Caithness 89, Orkney 67, Shetland 35 and Faeroes 19.

This impoverishment is not shown by the sea and shore birds. Nor is there a corresponding reduction in the other direction. Only two inland birds, snow bunting and redwing, breed regularly in the Faeroes but not Shetland; only one, the whimbrel, in Shetland but not Orkney; and only three, hen harrier, pintail and red-necked phalarope, in Orkney but not Caithness (but of these three the hen harrier bred formerly in Caithness and has been exterminated by man, and the pintail has bred there recently and may be establishing itself).

The main reasons for the progressive impoverishment seem to be two. First, the inland habitats are more varied on the mainland, and less varied the farther the islands are from the mainland. This particularly applies to woodland, bushes and gardens, but hardly at all to other habitats. Secondly, many of the species concerned have spread north only recently, a matter that is discussed later. The sea provides a temporary barrier to further spread. That this barrier is purely temporary is shown by the many species which have recently colonized Orkney and, to a less extent, Shetland, and by the numerous species which have bred occasionally in Orkney, Shetland and Faeroes without, as yet, becoming established. It is particularly difficult for a small island population to become established, as chance accidents may destroy the whole lot, and it may be some years before there is further colonization.

### (*b*) Inter-island distributions on Orkney

The Orkney archipelago contains one large island, Mainland, of 120,000 acres, about equal in area to all the other islands combined. There are 13 other islands of moderate size, mostly a few miles long, all containing much cultivated land, nearly all some moorland, and most with at least one or two reedy waters. The islands and their habitats are described in the faunistic paper, and in Table 4 of that paper the distributions of the inland species on these 14 main islands are tabulated. Details need not be given here, but certain points are of general interest.

Of the 67 regular land and fresh-water breeding species of Orkney all except three, dipper, common scoter and red-necked phalarope, breed on Mainland, while one irregular species breeding in 1941, the spotted flycatcher, did not nest on Mainland. But the distributions on the other 13 islands are much less uniform. In a number of cases this is due to habitat limitations. The woodland species are inevitably confined to Mainland, Hoy, Shapinsay, Rousay and Eday, as woods do not occur on other islands. The ducks, little grebe, coot, etc., are absent from Hoy, South Walls and Flotta, which lack suitable waters. The meadow pipit, various wading birds and the red grouse are absent or very local on some of the northern islands on which moorland is absent or very local. Red-throated divers breed only on those islands with moorland lochs, the short-eared owl only on those with thick ground vegetation and voles (*Microtus orcadensis*), and so on.

But even when full allowance is made for habitat requirements, many species are distributed among the islands very erratically. Suitable habitats for the rook occur on Shapinsay and Rousay, but it does not nest there; the jackdaw breeds on seven of the islands, and the other seven seem equally suitable; the pied wagtail is also local but could nest on every island; the mistle thrush might have been expected, but does not breed, on Hoy and Rousay; and the same applies to the song thrush on Stronsay, the stonechat and robin on Rousay, the dipper on Mainland, and the heron on many islands. The ducks, particularly wigeon, pintail, pochard and common scoter, also the little grebe and red-necked phalarope, breed on some islands with reedy waters, but not on others which appear equally suitable. Other similar examples are cited in the faunistic paper.

These erratic distributions are so common as to form a characteristic feature of the Orkney bird fauna. Omitting the cases in which habitat factors are involved, they occur mainly in species which have colonized Orkney in the last hundred years and are still spreading, e.g. rook, jackdaw, mistle thrush, stonechat, dipper, and the ducks. In such species it is to a large extent chance which island is colonized next. The absence of several increasing woodland species on Eday (greenfinch, chaffinch, willow warbler, mistle thrush, robin) is presumably because the Eday wood is of more recent origin than, and is relatively remote from, the other woods. More rarely, erratic distributions occur among species which are decreasing in Orkney, e.g. yellowhammer and sedge warbler, both now confined to Mainland, but formerly more widespread. The dunlin also fits in here, being formerly abundant but now scarce everywhere except, for no obvious reason, on Stronsay, where it is still abundant. A few long-established Orkney species, e.g. pied wagtail, heron, little grebe and red-necked phalarope, also show the same phenomenon.

The numerous small islands of Orkney were not considered in the analysis just given. These also show erratic distributions, linnet, corn bunting and song thrush being among the species which breed on some of them but which, despite suitable habitats, are absent from others.

A factor contributing to this phenomenon is the small size of many of the breeding populations. For example, the greenfinch was represented by about 12 pairs on Rousay, about six pairs on Shapinsay and two on Hoy; the chaffinch by about six pairs on Shapinsay, and two pairs on each of Hoy and Rousay; the linnet by some six pairs on Burray, two on each of Flotta and South Walls, one on Shapinsay; the reed bunting by under six pairs on Hoy, one on each of South Walls and North Ronaldsay; the song thrush by some five pairs on South Ronaldsay, four on Sanday and three on each of Burray and North Ronaldsay. Many similar examples could be quoted from the woodland and bush-frequenting species. And the same was true of pied wagtail, long-eared owl, birds of prey, many species of duck, the little grebe and red-throated diver, in which the total breeding populations for each island were in most cases under six pairs. Again, among the wading birds, the curlew,

dunlin, common sandpiper, golden plover and red-necked phalarope were represented by under ten pairs on each of several islands.

Each island population is isolated from the rest at least by the distance by sea between the islands, usually a few miles. In the case of the species frequenting inland waters and those frequenting bushes, the isolation is greater, as these habitats are local, and this applies more strongly to woodland species, since there are in Orkney only nine woods and four more areas of tall trees. Hence the woodland birds occur on island habitats within islands.

The breeding population on any one island is often so small that chance accidents or one bad season might destroy the whole of it. In such cases, owing to the isolation, it might well be a number of years before re-colonization took place. This has happened. The chaffinch bred on Hoy around 1859, not around 1888, but does so again now. Mistle thrush and robin once bred on Rousay, but do so no longer, while, on the other hand, they have colonized Shapinsay. The ring dove has recently colonized several new islands but has become extinct on Hoy. The red-necked phalarope has disappeared from the loch on Sanday where it bred for at least some 20 years, bred on Papa Westray for about two years recently, and has now colonized two new localities. The pintail has left Sanday but spread elsewhere. The jackdaw was breeding on Walls about 150 years ago, did not do so around 1880, but does so again now. Other similar instances could be cited.

The small size of most island breeding populations must help to produce the erratic inter-island distributions. On the other hand, the presence of a relatively large population of nearly all species on the centrally situated island of Mainland must exercise a stabilizing influence on the Orkney bird fauna. It is noteworthy that the Mainland populations do not appear to show such marked fluctuations as those of other Orkney islands.

### (*c*) FLUCTUATIONS

Comparison of the 1941 survey with those of Low in 1770, Baikie & Heddle in 1848 and Buckley & Harvie-Brown in 1891, indicates the very considerable alterations in breeding status which have occurred during 170 years.

#### *Colonization of Orkney*

The following 26 species colonized Orkney as breeding species after 1800. The date following the name of the bird gives the first year in which nesting was recorded; if there are subsequent dates breeding was irregular until the last date given (so far as recorded).

(1) *Woodland, tree and bush-frequenting species*

Rook (1876)
Greenfinch (1879)
Chaffinch (1839, 1859)
Yellow bunting (1855)
Willow warbler (before 1888)
Sedge warbler (1857)
Mistle thrush (1845, 1874, 1908)
Whinchat (*c.* 1885, after 1919)
Dunnock (1862)
Long-eared owl (1882, 1917)
Sparrowhawk (1886, 1914)
Ring dove (1840)
Pheasant (introduced)

(2) *Ducks*
Wigeon (before 1871, *c.* 1880)
Pintail (1908)
Shoveler (1892)
Pochard (1895)
Tufted duck (1888, 1895)
Common scoter (1927, 1941)

(3) *Other inland species*
Reed bunting (1839, 1848)
Stonechat (*c.* 1885)
Dipper (after 1919)
Mute swan (before 1888)

(4) *Sea birds*
Fulmar (1900)
Sandwich tern (1892)
Great skua (1916)

Hence since 1800, 26 breeding species have become established, of which 13 have become regular only in the last 50 years. In addition, a number of species, listed in Table 2, have bred sporadically during this period but have failed to become established. With 13 of the 26 species, colonization can be correlated with the planting of woods, gardens, trees and bushes in the nineteenth century, assisted in some cases, e.g. rook, greenfinch and ring dove, by the increase of land under cultivation. Six of the irregular species given in Table 2 (goldcrest, spotted and pied flycatchers, blackcap, common whitethroat, woodcock) are also woodland or garden birds.

The colonization by the six species of duck fits with the general marked increase of these birds as breeding species in Scotland (Baxter & Rintoul, 1922; Berry, 1939). The fulmar has also been increasing generally.

All these species have continued to increase and spread to new Orkney islands up to 1941 except for yellow bunting and sedge warbler, which have decreased markedly in the last 20 years, and stonechat and whinchat which markedly decreased (?temporarily) in 1941.

### *Colonizations of new Orkney islands*

In addition to these species, most of which have now spread to more than one island, the following eight species, already resident before 1800, have established themselves on new Orkney islands since 1891:

(1) *Inland species*
Jackdaw (Rousay, Calf of Eday, Westray)
Linnet (N. Ronaldsay)
Song thrush (N. Ronaldsay, Westray, Papa Westray)
Blackbird (N. Ronaldsay)

(2) *Sea birds*
Shelduck (Westray group)
Lesser black-backed gull (N. Ronaldsay)
Arctic skua (Papa Westray, Westray)
Black guillemot (N. Ronaldsay)

All these species except black guillemot have also increased markedly on those islands on which they were previously established. The spread of linnet, song thrush and blackbird is associated partly with the increase in bushes, woods and gardens, partly with their habitat adaptations (see later), and partly with the increase of land under cultivation. The last also applies to the jackdaw.

*Extinctions*

The following six inland species, formerly breeding regularly, have become extinct in Orkney:

Sand martin (regular till after 1890, only occasional since 1919)
Golden eagle (last *c.* 1840)
White-tailed eagle (last *c.* 1873)
Whooper swan (end eighteenth century)
Whimbrel (*c.* 1880, spasmodic since)
Ptarmigan (*c.* 1831)

Golden and white-tailed eagles, whooper swan and ptarmigan, were destroyed deliberately by man, the first two because they were thought to be destructive, the other two because they are edible.

*Other fluctuations*

A. The following five additional species have markedly increased:

(1) *Inland species*

Curlew
Redshank

(2) *Sea birds*

Eider
Great black-backed gull
Common gull

B. The following six inland species decreased markedly in the nineteenth century but have increased markedly in the twentieth:

Raven
Hen harrier
Short-eared owl
Red-throated diver
Peregrine falcon
Lapwing

In all six cases, the decrease was due directly to human destruction and the increase to human protection.

C. The following seven species decreased in the nineteenth century but have not continued to do so in recent times:

(1) *Inland species*

Heron
Snipe
Merlin
Red-necked phalarope
Kestrel
Golden plover

(2) *Sea birds*

Manx shearwater

Here also the decreases are attributable to direct human destruction, while in the case of snipe and golden plover the increase of agricultural land at the expense of moorland was certainly an important, and perhaps the chief, factor. Protection seems to have checked the decreases.

D. The following five inland species have decreased since 1890:

Yellow bunting
Dunlin (but not Stronsay, and partial recovery Mainland)
Sedge warbler
Wheatear
Red grouse

Decrease in the last case is due to human destruction, and in those of the wheatear and dunlin mainly to the increase of land under cultivation and, in the dunlin, also to egg-collecting.

E. Two other inland species have fluctuated:

The cuckoo, known in 1770, was apparently absent in 1793, was fairly common by 1888, but is not so common at the present time.

F. The common sandpiper increased in the nineteenth century but has markedly decreased in the twentieth.

G. The following nine summer visitors are present in greatly reduced numbers during cold or late summers:

(1) *Inland species*

Pied wagtail
Robin (see note below)
Whinchat
Stonechat
Swallow
House martin
Cuckoo

(2) *Sea birds*

Common tern
Arctic tern

All nine species were affected in the cold late summer of 1941. Buckley & Harvie-Brown noted the same effect for most of them in the cold wet summer of 1888. The species involved are predominantly insectivorous summer visitors, hence may be affected primarily through their food supply; but, at least in 1941, they also arrived from the south late and in greatly reduced numbers. The robin was tentatively included in this group, but actually the cold winter of 1940–1 may have had more effect on its numbers than the subsequent cold spring; Buckley & Harvie-Brown also record its decrease in Orkney after a cold winter.

H. One sea bird, the puffin, is subject to marked periodic reductions through disease.

*Species not recorded as fluctuating*

(1) 17 *inland species*

Hooded crow, starling, twite, corn bunting, house sparrow, skylark, meadow pipit, wren, mallard, teal, little grebe, rock dove, black-headed gull, corncrake, moorhen, coot, water rail.

(2) 11 *sea and shore birds*

Rock pipit, red-breasted merganser, cormorant, shag, storm petrel, ringed plover, oystercatcher, herring gull, kittiwake, razorbill, guillemot.

But of these, four inland species, starling, corn bunting, house sparrow and corncrake, can safely be taken as having increased in the nineteenth century with the marked increase of land under cultivation. And one inland species, the meadow pipit, can safely be taken as having greatly decreased with the great decrease in moorland, especially on the northern islands. One sea bird, the herring gull, has almost certainly increased with the increase in shipping and the decrease in the taking of gulls' eggs for food. Water rail and storm petrel feature in this category because they are so difficult to observe that no assessment of their numbers has ever been made. The remaining species were simply recorded as common by the various writers on Orkney birds. Hence, while no drastic change can have taken place in their numbers, it would be possible for any of them to have, say, doubled or halved in numbers, during the last 100 years.

*Irregular breeders*

To complete the list of species which have fluctuated, the irregular breeding species should be included. These include the eight certain and 12 more doubtful species listed in Table 2. Also, as shown earlier, at least nine of the 26 species which have colonized Orkney since 1800 bred irregularly before they became established; and sand martin and whimbrel have bred irregularly since they ceased to be regular.

*Summary of fluctuations*

Table 3. *Fluctuations of Orkney breeding birds*

| | Inland species | Sea and shore birds |
|---|---|---|
| Colonized Orkney after 1800: | | |
| (*a*) since increasing | 19 | 3 |
| (*b*) since increasing, but reduced after bad year | 2 | . |
| (*c*) since decreasing | 2 | . |
| Others markedly increased since 1800 | 6 | 7 |
| Increased nineteenth, decreased twentieth century | 2 | . |
| Decreased nineteenth century, stable or increased since | 12 | 1 |
| Decreased since 1890 | 3 (+2) | . |
| Extinct | 6 | . |
| Periodic decreases | 4 (+3) | 3 |
| Obviously increased but not proved | 4 | 1 |
| Obviously decreased but not proved | 1 | . |
| Total which have changed markedly | 61 | 15 |
| Total which have not changed markedly | 11 | 9 |
| Unobservable | 1 | 1 |
| Total of regular and formerly regular species | 73 | 25 |
| Irregular species | 8+ | . |

The table shows that of the 73 regular and formerly regular inland breeding species of Orkney, as many as 61 (84 %) have changed markedly in status in the last 100 years. Of the 25 sea and shore birds, 15 (60 %) have changed markedly in status in the same period. This does not take account of the irregular breeding species, whose inclusion would considerably raise the percentage of fluctuating species; but, owing to doubtful records, the precise number cannot be given.

*Causes of fluctuations*

The four main assignable causes for species which have increased are:

(1) Growth of woods and bushy areas (16 cases).

(2) Increase of land under cultivation (seven or more cases).

(3) Protection (six cases, also subsidiary cause in many other cases and has prevented further decrease in many more).

(4) Habitat adaptations (four cases—in two others it has not as yet made much difference).

The three main assignable causes for species which have decreased are:

(1) Direct human destruction (in 20 cases a major factor).

(2) Decrease of moorland (nine cases).

(3) Periodic cold winters or late springs (eight or nine cases).

But the marked fluctuations of a number of species are not referable to any of these factors. 16 species whose increase cannot be correlated with any obvious environmental factor are: reed bunting, stonechat, dipper, seven species of ducks (assisted, but not initiated, by protection), fulmar, curlew (despite the reduction in moorland), redshank, sandwich tern, common gull, and arctic skua. Five species whose decrease cannot be correlated with any obvious environmental factor are yellow-hammer, sedge warbler, sand martin, whimbrel (certainly not due primarily to human destruction or decrease of moorland), and common sandpiper.

### (*d*) Habitat adaptations

The blackbird, perhaps the most typical British woodland bird, is in Orkney also characteristic of open fields and low-lying moorland away from all trees, bushes, gardens and rocks, in haunts typically associated with the skylark. Colonization of open country occurred between the years 1890 and 1910, and is now found on every Orkney island. The song thrush, another typical British woodland and garden bird, shows a similar habitat change on Westray and Papa Westray but not, as yet, elsewhere (save doubtfully on Mainland). On Westray the habitat change originated after 1890 and on Papa Westray in the last two or three years. Similarly the bush-frequenting linnet breeds away from all bushes on Westray, Sanday and Stronsay, but not, as yet, elsewhere, and this again seems a habit of recent origin. And the ring dove, which typically nests in trees, some 20 years ago began to breed regularly on the ground in heather on Mainland, and at least occasionally does so on Rousay.

The normal fixity of habitat selection in birds is well known, and changes are highly unusual (Lack, 1933, 1937, 1940). These four species feed mainly on the ground, and there has been no change in feeding habitat, save slightly in the case of the linnet. The adaptation has been primarily of general breeding habitat, in the selection of which the psychological factor plays so big a part. In each case it has occurred after a marked increase in numbers of the species, correlated with a marked increase in the normal breeding habitat in Orkney. The latter seems to have started the increase in numbers, and later the species has overflowed.

Traces of the change occur elsewhere in Britain. The blackbird regularly builds on the ground in Devon woods, the song thrush rarely, and both species sometimes nest in stone quarries or steep rocky valleys almost or quite devoid of bushes; while this is their regular habitat on Ailsa Craig (J. Fisher, in litt.). In Orkney the change is much more marked, as the birds breed in flat open country. The Hebridean song thrush breeds in open country, and the ring dove sometimes breeds in heather in Wales (Witherby and others 1940), so that the full habitat adaptations found in Orkney have arisen independently in a few other places.

The fulmar petrel normally nests on sea cliff ledges and on the flat tops of small cliff-bound stacs and islets. On North Ronaldsay several pairs nested on stone walls set back several hundred yards from the sea; and, much more remarkable, on Sanday several pairs nested on sand-dunes up to several hundred yards from the sea, a habit probably spreading to Stronsay. A still more unusual departure may be occurring if the pairs resident on the stone walls round the fresh-water Tredwell Loch on Papa Westray start to nest; indeed that they occur at all on fresh water is highly unusual. The fulmar's habitat changes, like those of the other species mentioned, have followed a rapid increase in the numbers of the species.

The rock pipit is typically confined to rocky coasts. The stone walls along the flat sandy shores of Sanday and North Ronaldsay, where the rock pipit also breeds, obviously count as cliffs so far as the bird is concerned. But its breeding in stone walls round the fresh-water Tredwell Loch, Papa Westray, out of sight of the sea, in pasture and arable land, is surprising. Rock pipits may also have nested on a moorland headland on Westray 150 yards from the cliffs. Elsewhere in Orkney the species is confined to the cliffs, hence the habitat changes are very local. Nesting on rocky moorland is also recorded on several other British islands, Foula, St Kilda and the Outer Hebrides, though nowhere on the mainland [J. Fisher, in litt.; Harrisson & Lack, 1934; Witherby and others 1938].

Another instance of a habitat change on islands is afforded by the wren, which is typically a bush, scrub and woodland bird, also occurring by moorland streams. In the Shetlands, Fair Isle and St Kilda, its characteristic habitat is the tall sea cliffs. Except very locally, the wren does not frequent sea cliffs in Orkney.

To summarize, seven cases of marked habitat change locally on small islands are mentioned in this section, which is interesting in view of the difficulty I had in finding any such cases in earlier discussions of the subject.

## PART 2. OTHER SMALL BRITISH ISLANDS

### INTRODUCTION

The following survey was done in order to find out which features of the Orkney bird fauna applied to other British small islands. Unfortunately the literature on small islands is very scattered, hence before entering on a general discussion, it is necessary to provide a summary of the bird fauna of each island. It is hoped that these summaries are correct, but in most cases personal knowledge of the island is lacking, hence treatment is inevitably less critical than it was for Orkney. Only the more remote British small islands are considered, and of these only the ones which are better documented.

In Part 3 the sea birds are considered separately from the land and fresh-water species. The same division is made as for Orkney, and it was not thought

necessary to separate them in the following summaries. However, in each category all sea and shore birds are listed after the land and fresh-water species, the order being the same as that used in Table 1.

### *Fair Isle*

Fair Isle, some three miles long and two broad, lies 23 miles from North Ronaldsay and rather closer to Shetland. Clarke (1912) gave a list of breeding birds, and G. Stout supplied one in 1936 to L. S. V. Venables (private communication). With one more species, the house martin, recorded by J. Wilson (E. V. Baxter & L. J. Rintoul, in litt.), the following is probably a complete list of breeding birds for the last 30 years.

*Regular breeders:* 26. Raven, hooded crow, starling, twite, house sparrow, skylark, meadow pipit, wheatear, wren, peregrine falcon, corncrake; rock pipit, eider, shag, storm petrel, fulmar (colonized 1902), ringed plover, oystercatcher, herring, lesser and great black-backed gulls, kittiwake, razorbill, guillemot, black guillemot, puffin.

*Regular by* 1936, *but not in* 1912*:* 5. Rock dove (extinct by 1912, now recolonized), snipe (colonized 1923); common gull, great skua, arctic skua (bred till 1905, now recolonized).

*Occasional breeders:* 14. Corn bunting (ceased by 1936), tree sparrow, white and/or pied wagtail, song thrush, redwing, blackbird, swallow, house martin, golden plover, lapwing, moorhen, quail; red-breasted merganser, cormorant.

*Doubtful:* Ring ousel, cuckoo.

### *Foula*

This small island lies 12 miles west of the main Shetland group. The following provisional list was obtained by J. Fisher and L. S. V. Venables who made a 36 hr. visit in June 1938 (private communication).

*Breeding species:* 30. Probably as for *regular* species listed for Fair Isle, but with blackbird and Manx shearwater and without ringed plover and common gull. Also great black-backed gulls, though seen, were not proved to breed. One additional species, the swallow, bred in 1924 (Bishop, 1931).

### *Shetlands*

These lie 50 miles from Orkney, with Fair Isle between, and extend over some 70 miles. As compared with Orkney there is much more moorland, much less cultivated land, no woods, relatively few gardens with trees. Saxby (1874) wrote the first comprehensive survey of the northern islands, Buckley & Evans (1899) of that of the group as a whole. Little has been published in the last 30 years. Hence knowledge of both past and present status is inadequate.

*Regular breeders:* 60. These are listed in Table 1.

*Formerly regular, now extinct:* 3. Hen harrier, white-tailed eagle, whooper swan.

*Irregular and occasional breeders:* 14. Chaffinch, snow bunting, tree sparrow, pied and/or white wagtail, willow warbler, blackcap, redstart, swallow, house martin, sand martin, cuckoo, short-eared owl, quail; Sandwich tern.

*Doubtful:* Heron, black-throated diver, woodcock, greenshank and others.

*Nine regular species are recent colonists,* four arriving before 1900: Wigeon, lapwing, moorhen; fulmar; five arriving after 1900: pintail, common scoter; shelduck (bred formerly, later extinct, recently recolonized), gannet and common tern.

*At least seven other species have greatly increased* since 1874: Song thrush, blackbird, curlew, common sandpiper, redshank; black-headed gull, great skua.

*At least one other species,* the whimbrel, *has greatly decreased.*

The 16 species which have colonized and increased in Shetland have also increased in Orkney except perhaps for moorhen and common tern, the past and present status of which in Orkney are not sufficiently known for conclusions to be drawn. The four species which have decreased have also decreased in Orkney.

### *Sule Skerry*

About half a mile long and 35 acres in extent, this lies 35 miles west of Orkney and 32½ miles from the mainland of Scotland. No land birds breed.

Thirteen species bred in 1903: Rock pipit, eider, shag, storm petrel, oystercatcher, arctic tern, herring and great black-backed gulls, kittiwake, razorbill, guillemot, black guillemot and puffin. Later, the fulmar and lesser black-backed gull have colonized, but the former is again extinct (Tomison, 1904; Stewart, 1938).

### *North Rona*

This is 47 miles from Scotland and a similar distance from the Outer Hebrides. There have been seven brief ornithological visits. The table of fluctuations given by Harrisson (1932) is somewhat inaccurate. With the later data of Ainslie & Atkinson (1937) the following summary is given:

*Regular breeding species:* 18. Starling, wheatear; rock pipit, eider, shag, storm and fork-tailed petrels, fulmar, oystercatcher, arctic tern, herring, lesser and great black-backed gulls, kittiwake, razorbill, guillemot, black guillemot (possibly absent some years), puffin. Of these starling, fulmar and perhaps arctic tern and lesser black-backed gull colonized after 1883, and the great black-backed gull has fluctuated.

*Occasional breeding species:* 2. Tree sparrow (1886), peregrine falcon.

*Doubtful:* Hooded crow, meadow pipit, ringed plover, whimbrel.

### *Eilean Mhor*

This is one of the Flannan Islands, 16 acres in extent, 20 miles out from the Outer Hebrides. According to Clarke (1905), 17 species breed.

The list is the same as that for the regular species on North Rona, together with raven, twite and peregrine falcon, and without starling, arctic tern, lesser black-backed gull and black guillemot. However, the last was seen but not proved to breed, as was hooded crow; while whimbrel has also probably bred. Lesser black-backed gull and probably cormorant breed on others of the Flannans.

### *St Kilda*

Another isolated island group, lying 40 miles west of the Outer Hebrides. There are at least ten detailed accounts of the birds, the first in 1698, the rest between 1840 and 1939.

*Regular species:* 27. As for Fair Isle, but with gannet, fork-tailed petrel and Manx shearwater, and without house sparrow, skylark, corncrake, ringed plover, common gull, great and arctic skuas.

Raven, hooded crow, meadow pipit, peregrine falcon, common snipe, eider, lesser black-backed gull and black guillemot are usually represented by under ten pairs.

*Formerly regular, now extinct:* 9. Corn bunting (1840), tree sparrow (1885–1911), song thrush (1840, 1847), kestrel (1840); white-tailed eagle (nineteenth century), cormorant (1840–1885), common gull (1840, 1847), great auk (late eighteenth, early nineteenth century). For corncrake, see next section.

*Occasional breeders:* 2. Snow bunting (1913), corncrake (regular to 1840).

*Doubtful breeders:* 2. Dunlin (1840), golden plover (1939).

*Nine other species have fluctuated markedly:* Hooded crow (decrease), starling (decrease 1931, increase 1939), meadow pipit (increase), wren (decrease late nineteenth century, increase later), rock dove (bred till 1885, recolonized by 1931), common snipe (colonized 1900, increasing); eider (increase), fulmar (presumed increase), and lesser black-backed gull (usually rare, many 1885).

*Outer Hebrides (excluding St Kilda, North Rona and Flannan Islands)*

This group, some 130 miles in length, come within 15 miles of Skye at one point, but most parts are considerably further from any other land. Moorland is much more extensive than in Orkney, and there are mountains. Woods occur at Rodel and a few other points in Harris and more recent plantations at Stornoway in Lewis. The present status of the birds is relatively well known and is summarized by Witherby and others (1938–41); while records go back over a hundred years. Unfortunately the nineteenth century records are often so vague that it is much harder to assess fluctuations here than in Orkney.

*Regular breeding species:* 94. These are the same as the 92 regular breeders listed for Orkney in Table 1, but omitting eight species and with ten additions. The ten additions are: tree sparrow, goldcrest, common whitethroat (occasional O.), golden eagle (extinct O.; still classed by Witherby and others as resident in O.H., though Baxter & Rintoul (in litt.) have no recent record), common buzzard, grey lag goose, scaup, black-throated diver, greenshank; and little tern. The eight omissions are: yellow bunting (formerly O.H., now extinct), swallow (occasional O.H.), house martin, long-eared owl, sparrowhawk, common scoter, curlew; and great skua.

*Occasional breeders:* 8. Carrion crow, lesser redpoll, coal tit, spotted flycatcher, redstart, whimbrel, woodcock, quail; tawny owl has been seen in summer, and other species have been recorded doubtfully.

*Formerly regular, now extinct:* 5. Chough, yellow bunting, sand martin, white-tailed eagle, ptarmigan (apparently).

*Colonized since* 1842*:* 22. Ten before 1900: Rook, jackdaw, tree sparrow, willow warbler, common whitethroat, pochard, scaup, ring dove; fulmar, little tern. 12 after 1900: linnet, pied wagtail, goldcrest, sedge warbler, mistle thrush, common buzzard, heron, wigeon, pintail, shoveler, tufted duck; Sandwich tern.

*Also increased markedly:* 9. Chaffinch, greenfinch, house sparrow, song thrush, blackbird, robin, dunnock; shelduck, eider.

*Decreased markedly:* 4. Golden eagle, hen harrier, grey lag goose, red-necked phalarope.

Of the 31 species which have colonized or markedly increased, at least 22 have also markedly increased in Orkney, and of the nine which have markedly decreased, seven have markedly decreased in Orkney and the other two are unknown there.

*Some Inner Hebrides*

(1) *Coll*, over 12 miles long, about 3 miles broad, lying some 8 miles from the mainland, but with Tiree 2 miles away, has a list of Passerines not dissimilar to those of Orkney and the Outer Hebrides, but with some gaps, mainly correlated with the absence of woods save for a few sycamores. From MacDougall's (1938) survey it appears that of land and fresh-water species, 42 breed regularly of which 20 are represented by under ten pairs each, while an additional 12 species have bred. 14 species of sea birds breed regularly, one being under ten pairs strong.

(2) *The Small Isles*, i.e. Canna, Muck, Rhum and Eigg, are relatively well wooded compared with Orkney. Eigg lies 8 miles from the mainland, Rhum 6 miles south of Soay off Skye. The birds of Eigg have been described in five papers, starting in 1885, but too vaguely for determination of fluctuations. Woodland and garden breeding species in these islands include: lesser redpoll, greenfinch, chaffinch, goldcrest, blue tit, long-tailed tit, spotted flycatcher, willow warbler, wood warbler, common whitethroat, robin, dunnock and woodcock—a richer assembly than are found in the Outer Hebrides or Orkney, and suggesting which species may colonize the latter next.

### *Ailsa Craig*

This islet, some 1½ miles in circumference, lies in the Clyde estuary 8½ miles from the nearest land.

*Breeding species:* 21. Raven, house sparrow, meadow pipit, song thrush, blackbird, wheatear, dunnock, wren, peregrine falcon; rock pipit, cormorant, gannet, fulmar, oystercatcher, common, herring and lesser black-backed gulls, kittiwake, razorbill, guillemot and puffin. In addition the twite has bred, and starling and rock dove are seen in summer but not known to nest (J. Fisher, private communication).

### *May*

This lies in the Firth of Forth 5 miles from the mainland, and is over a mile long by a quarter of a mile wide. Baxter & Rintoul (1925) give data over many years, amplified in litt., including complete censuses for 1921 and 1924. Southern (1938) took a census in 1936.

*Regular breeders, stable* 1921–36*:* 1. Oystercatcher (increased before 1921).

*Regular breeders, recently colonized, increasing:* 6. House sparrow; fulmar, Sandwich, common and arctic terns, lesser black-backed gull.

*Other regular breeders markedly increasing:* 3. Shag, herring gull, kittiwake.

*Formerly regular, now extinct:* 3. Tree sparrow, rock dove; black guillemot.

*Other regular breeders markedly decreasing:* 3. Meadow pipit, wheatear; rock pipit.

*Regular breeders, markedly fluctuating:* 6. Starling, pied wagtail; eider, razorbill, guillemot, puffin.

*Occasional breeders:* 10 (11). Carrion crow, linnet, willow warbler, song thrush, blackbird, dunnock, peregrine falcon, redshank, lapwing, moorhen. Also a doubtfully wild pair of rock doves bred in 1911.

*Of the* 19 *regular breeders, ten are usually represented by under ten pairs each:* Starling, house sparrow, meadow pipit, pied wagtail, wheatear; shag, fulmar, oystercatcher, Sandwich tern, lesser black-backed gull.

### *Isle of Man*

Some 32 miles long and up to 13 miles wide, Isle of Man is at its nearest 16 miles from Scotland, 28 from England, 27 from Ireland and 42 from Wales. It contains many woods, mostly planted in the last 150 years. Ralfe (1905) lists 88 breeding species, of which 72 are land and fresh water and 16 sea and shore birds. These will not be listed here, except for

*Colonists,* 1830–1905*:* 9–11. Tree sparrow, great tit, blue tit, spotted flycatcher, chiffchaff, wood warbler, stock dove; little tern, common gull. Also probably crossbill (breeding not proved) and tree creeper (breeds now, possibly overlooked in past).

*Colonists*, 1906-1939: 15–16. Carrion crow, coal tit, blackcap, garden warbler, whinchat, short-eared owl, barn owl, woodcock, common sandpiper, redshank; fulmar, Sandwich and common terns, great black-backed gull. Also probably lesser whitethroat; while the heron, which had become extinct by 1905, had recolonized. Some of these species are not yet established (Ralfe, 1923, 1924–35).

*Formerly regular, now extinct:* 4. White-tailed eagle, bittern, blackcock; Manx shearwater. The blackcock was probably an artificial introduction. In addition heron became extinct but recolonized, red grouse became extinct and was reintroduced, and perhaps no genuine wild rock doves remain.

*Probably have bred, not proved:* 3. Crossbill, lesser whitethroat, golden plover.

There are some curious gaps in the bird fauna as compared with the neighbouring mainlands: jay, bullfinch, yellow wagtail, coal tit (till 1908), long-tailed tit, whinchat, tawny owl, and barn owl till recently.

### *Bardsey*

This is 2 miles long by ¾ mile wide and lies 2 miles off the coast of north Wales. Four visits have been paid, in 1902, 1905, 1913 and 1933.

*Breeding on all visits:*

(*a*) *Over ten pairs:* 11. Jackdaw, starling, linnet, house sparrow (colonized 1789), corncrake; rock pipit, Manx shearwater, oystercatcher, herring gull, razorbill, guillemot.

(*b*) *Under ten pairs:* 14. Raven, carrion crow, chough, corn bunting, meadow pipit, pied wagtail, sedge warbler, blackbird, wheatear (? overlooked 1913), dunnock, swallow, cuckoo, peregrine falcon, lapwing.

*Breeding irregularly:* 13. Chaffinch (1902), skylark (1933), spotted flycatcher (1902), willow warbler (1902), whitethroat (1902, 1905), mistle thrush (1913), song thrush (1913), stonechat (1905–33), robin (1913), wren (1913–33), moorhen (1913); ringed plover (1933), great black-backed gull (1913). In some of these cases, breeding was presumed only.

*Doubtful breeders:* 3. Kestrel (1933), redshank (1913); shag (1913, 1933).

### *Skokholm*

This island, 240 acres in extent, lies 3 miles off the south-west coast of Wales. Lockley (1935–39) has done an annual breeding census since 1925.

*Regular breeders. Over ten pairs:* 13. Carrion crow, meadow pipit; rock pipit, wheatear, storm petrel, Manx shearwater, oystercatcher, herring, lesser and great black-backed gulls, razorbill, guillemot, puffin.

*Regular breeders. Under ten pairs:* 6. Raven, skylark, dunnock, lapwing, moorhen; shag.

*Breeding, but not every year:* 18. Chough, linnet, pied wagtail, sedge warbler, common whitethroat, blackbird, robin, stonechat, swallow, cuckoo, little owl, peregrine falcon, common buzzard, mallard, teal (probably), common snipe, corncrake, water rail.

One species, common tern, is known to have bred before 1925.

### *Steep Holm*

In the Bristol Channel 3 miles from land and ½ mile long, 300 yd. wide. From Lewis (1936) and Tetley (1937) the following summary can be made:

*Regular breeders. Over ten pairs:* 4. Cormorant, shelduck, herring and lesser black-backed gulls.

*Regular breeders, a number:* 3. Meadow pipit, blackbird; rock pipit.

*Breeding, but not each year:* 11. Carrion crow, starling, linnet, skylark, spotted flycatcher, common whitethroat, song thrush, wheatear, kestrel, mallard; oystercatcher.

*Breeding, under ten pairs, and perhaps not every year:* 6. Raven, robin, dunnock, wren, peregrine falcon, great black-backed gull.

*Doubtful:* 1. Little owl.

Lewis is not very precise in his statements, so some of the above species have to be put in vague categories and some may be wrongly placed. But probably of 24 breeding species 18–20 species are represented by under ten pairs each and 11–13 of these do not breed every year.

### *Lundy*

This lies some 12 miles off the north Devon coast, and consists of 1116 acres, being some 3 miles long and rather over ½ mile broad. Loyd (1922, 1925) summarizes information up to these dates, and provides the first comprehensive survey. Harrisson (1932) and WynnesEdwards & Harrisson (1932) made a census in 1930, and Perry (1940) another in 1939. The following summarizes the breeding species. The previous survey by Harrisson (1932) needs considerable modification.

*Regular breeders. No evidence for marked change.*

(*a*) *Over ten pairs:* 9. Skylark, meadow pipit; rock pipit, Manx shearwater, herring gull, kittiwake, razorbill, common guillemot, puffin.

(*b*) *Under ten pairs:* 10. Raven, chaffinch, song thrush, robin, swallow, cuckoo, peregrine falcon, kestrel, ring dove, pheasant.

*Regular breeders. Increased.*

(*a*) *Now over ten pairs:* 5. House sparrow (colonized *c.* 1900); shag, oystercatcher, lesser and great black-backed gulls (colonized 1895).

(*b*) *Now under ten pairs:* 3. Buzzard, lapwing (colonized 1927). Also carrion crow probable increase.

*Regular breeders. Decreased.*

(*a*) *Now over ten pairs:* 1. Blackbird.

(*b*) *Now under ten pairs:* 4. Linnet, common whitethroat. Also corncrake and gannet (now erratic).

*Regular breeders. Fluctuated:* 3. Stonechat (over ten pairs), dunnock (in some years over ten pairs), pied wagtail (under ten pairs).

*Regular breeders. Evidence for fluctuations doubtful:* 3. Wren (over ten pairs), wheatear (under ten pairs); cormorant (over ten pairs).

*Breeding some years not others:* 17 (15). Hooded crow, starling, goldfinch, yellow bunting, yellow wagtail, goldcrest, willow warbler, blackcap, whinchat, sand martin, sparrowhawk, mallard, common snipe, dunlin, corncrake (formerly regular), quail; gannet (formerly regular).

*Doubtful breeding records:* House martin, swift, teal (personal record 1934), turtle dove, curlew, water rail, moorhen and other species listed by Loyd.

*Extinct:* 3. Chough, white-tailed eagle, rock dove.

### *The Scillies*

This group of islands, scattered over some 10 miles of sea, lies 22 miles off Cornwall. Clark & Rodd (1906) provide the first good summary, but this and the several subsequent accounts are too vague for adequate estimates of fluctuations.

*Regular breeders, no evidence for marked change:* 26. Corn bunting, skylark, meadow pipit, sedge warbler, song thrush, blackbird, wheatear, stonechat, robin, dunnock, wren, swallow, kestrel, corncrake, moorhen, coot; rock pipit, cormorant, shag, storm petrel, Manx shearwater, ringed plover, oystercatcher, lesser black-backed gull, razorbill, puffin.

*Regular breeders, recently colonized:* 10. Starling, greenfinch, chaffinch, house sparrow, great tit, goldcrest, mistle thrush, ring dove, pheasant (introduced); shelduck.

*Extinct but now re-established:* 1. Kittiwake (1900, 1937).

*Regular breeders, marked increase:* 3. Linnet; herring and great black-backed gulls.

*Regular breeders, marked decrease:* 4. Peregrine falcon, mallard; common tern, guillemot.

*Extinct:* 5. Raven, carrion crow, chough; Sandwich and arctic terns.

*Extinct, but occasional since:* 2. Black-headed gull (1845, 1925), roseate tern (1867, 1924).

*Erratic:* 2. Pied wagtail, quail.

*Sporadic:* 2. Tree pipit, nightjar.

## PART 3. GENERAL FEATURES OF THE BIRD FAUNAS OF BRITISH SMALL ISLANDS

### A. Descriptive

#### (*a*) *Introduction*

The phenomena discussed here refer primarily to the land and fresh-water species, but the sea birds are also of interest, particularly as they provide a standard by which to estimate the land and fresh-water species. Hence, in what follows, two sets of figures are given, the first referring to the land and fresh-water species (as differentiated in Table 1), and the second set, which is placed in brackets after the first, referring to the sea and shore birds.

#### (*b*) *Characteristic features*

The following seem the characteristic features of the inland breeding bird populations of British small islands:

(1) *Marked and unusual habitat adaptations*

Seven cases are given in Part 1.

(2) *Small total size of breeding populations*

This applies to most land and fresh-water species, especially on the smaller islands. Thus on St Kilda five out of ten[1] (three out of 17) regular breeders are represented by under ten pairs each, on Coll 20 out of 42 (one out of 14), on May five out of five (five out of 14), on Bardsey 14 out of 19 (none out of six), on Skokholm five out of eight (one out of 11), on Lundy 17–18 out of 24 (one out of 12), and on Steep Holm the great majority, but an exact figure cannot be given. Figures for numerous inland species on the smaller Orkney islands were given in Part 1. For larger islands figures are not available.

*Note.* The above figures refer only to regular breeders. Had irregular breeders been included, the totals of species under ten pairs strong would have been raised considerably.

[1] The inland species, followed by the sea birds in brackets, as already explained. Similarly throughout.

(3) *Numerous erratic breeders*

The high proportion of species which do not breed every year is best shown by the data from small islands watched regularly. On Skokholm as many as 18 out of the 26 species (none out of 11) which have bred in a 15-year period have not bred every year, and this applies to 12 out of 25 (two out of 22) on Fair Isle and 11 out of 17 (none out of 15) on May over rather longer periods. Bardsey, Lundy and Steep Holm have been watched much less regularly, but on Bardsey 11 out of 30 (two out of eight), on Lundy at least 16 out of 40 (one out of 13) and on Steep Holm 10–12 out of 18 (one out of six) are occasional breeders. At least 12 species have bred irregularly on Coll.

In Shetland 13 (one) species, or more if doubtful records are included, in Orkney between eight and 20 species, and in the Outer Hebrides eight or more species have bred irregularly. In Orkney nine other species, formerly irregular, are now established, and two others now irregular were formerly regular. These archipelagos have been watched much less intensively than the small islands noted above, and there are a number of doubtful records, so that the totals of occasional breeders are really larger.

(4) *Frequent colonization*

In Orkney 23 out of 73 (three out of 25) regular and formerly regular breeding species have become established since 1800, in Shetland five out of 38 (four out of 25), in the Outer Hebrides 19 out of 75 (three out of 25), in Scilly nine out of 31 (two out of 20) and in Isle of Man 17–20 out of 87–89 (six out of 20).

Colonization and establishment is also recorded on the small islands, e.g. two out of 13 (four out of 18) on Fair Isle, one out of two (one, perhaps three, out of 16) on North Rona, three (tree sparrow, common snipe, rock dove) out of ten (none out of 17) on St Kilda, one out of five (five out of 19) on May, two out of 28 (one out of 13) on Lundy. Hence colonization would appear to be less on small than large islands. This is partly because one cause of recent colonization has been the planting of trees, which has occurred mainly on the large islands; but partly, also, because species which colonize small islands usually fail to establish themselves, and so have been classified not as colonists but as irregular breeders in this analysis. Also, the records go back less far for small islands (except St Kilda).

(5) *Extremely marked fluctuations*

In Orkney at least 61 out of the 73 (84 %) of the *regular* breeding land and fresh-water species have shown marked fluctuations (and 15 out of 25 sea birds), in Shetland at least 15 out of 38 (five out of 25), in the Outer Hebrides at least 35 out of 75 (five out of 21), in the Scillies at least 15 out of 31 (ten out of 20). Except for Orkney, the data are very incomplete; so the proportion showing fluctuations should probably be much higher. Few smaller islands have been watched sufficiently long, but on St Kilda at least 13 out

of 17 (six out of 20) regular and formerly regular breeders, on May seven out of seven (15 out of 15) and on Lundy at least 14 out of 28 (five out of 13) have fluctuated markedly.

*Note.* The species classed as irregular breeders were not included in the totals given above, which would considerably raise the proportion of species which have fluctuated.

(6) *Irregular distributions*

In many cases, the presence of a species on one island and its absence on another is not attributable to habitat or other environmental differences. Thus the common gull breeds on Fair Isle but not on Foula or St Kilda. Skylark and song thrush might have been expected but do not breed on St Kilda. Comparing Orkney and the Outer Hebrides, one might have expected tree sparrow, common whitethroat, scaup, greenshank and little tern to breed regularly in the former, and the eight species regular in Orkney but not the Outer Hebrides might all have been expected in the latter. Jackdaw and starling are absent on Lundy and Skokholm but breed on Bardsey, and the starling but not the jackdaw, breeds in the Scillies. Many similar examples were given comparing different Orkney islands. Most cases refer to land and fresh-water species, but a few to sea birds.

(7) *Gaps in the bird faunas*

Similarly, even discounting all cases due to habitat limitations, the islands in every case possess fewer land and fresh-water species than does the nearest mainland. This was shown in Part 1 for Orkney as compared with Caithness, while the more remote Shetlands and Faeroes showed further reductions. Instances were also given for Isle of Man, and, as can be seen from the other island lists, the smaller and more isolated an island, the larger the number of gaps among land and fresh-water species which, from habitat considerations, might be expected to breed.

## B. Factors involved

### (*a*) *Causes of marked fluctuations*

(1) *Human activities*

*Planting of woods, bushes and gardens.* This accounts for the spread of woodland, bush and garden birds to Orkney (13), Outer Hebrides (7), Inner Hebrides, Isle of Man (10–12) and Scilly (5), during the last hundred years. There was presumably a corresponding exodus of woodland birds from some of these islands at the more distant period when the natural forest disappeared.

*Increase of agricultural land.* This applies much more to Orkney than to the other islands considered here and has been discussed.

*Modification of moorland* by peat cutting and grazing has caused decline of moorland species, especially in Orkney.

*Human destruction and protection.* This accounts for the nineteenth-century decrease, and in some cases extinction, of larger birds of prey, larger edible species such as whooper swan and grey lag goose, and collectors' rarities such as red-necked phalarope. In the twentieth century, protection has predominated over destruction, so those species which were not by then extinct have mostly increased.

*Human introductions.* These have been very few: pheasants successfully on several islands, red grouse in Shetland and (reintroduced) in Isle of Man, common partridge on several islands unsuccessfully. The first pochard breeding in the Outer Hebrides had perhaps escaped from captivity.

(2) *Small size of populations*

The liability of small populations to accidental extinction and the delay in recolonization due to isolation is alone sufficient to account theoretically for many cases of fluctuations, especially on small islands, where many land and fresh-water species are represented by under ten pairs each, and where species repeatedly colonize and die out.

(3) *Wide-scale natural fluctuations*

But other fluctuations not attributable to human factors occur over wide areas, such, for example, as the widespread increase of the starling, jackdaw, various species of duck, the fulmar, and the great black-backed gull, and the widespread decrease of the chough, corn bunting (Fair Isle, several Inner Hebrides, etc.), yellow bunting (Orkney, Outer Hebrides), sand martin (Orkney, Outer Hebrides, etc.), whimbrel (Orkney, Shetland) and others. Some of these cases may have been assisted by human or other environmental factors, but these were not the main cause. Some cases may be due to less obvious environmental change. Another possibility is an internal change within the species. One type of change within the species which has certainly led to a marked increase in numbers is the habitat change of linnet, song thrush, blackbird and ring dove in Orkney.

(4) *Fluctuations in sea birds*

From the preceding sections, it is clear that the fluctuations of sea birds on small islands are not on a scale in any way comparable with those of land and fresh-water species. This is explicable partly through the much smaller, though by no means negligible, influence of changing human factors, and partly through the fact that nearly all the sea birds are represented by relatively large populations which, moreover, are not much isolated from each other, as the birds feed on the intervening seas.

### (*b*) *Irregular distributions*

Apart from cases due to habitat differences, irregular distributions between islands are due partly to the small size of island populations and their liability to accidental extinction, and partly to the irregular manner of spread of an increasing species, as shown, for example, by the jackdaw in Orkney.

### (c) *Gaps in the bird faunas*

That invariably fewer inland species breed on islands than on the adjacent mainland is due in some cases to habitat differences, in others to the liability to extinction of small island populations, and a third important factor is the relative difficulty, as compared with the mainland, of colonization and establishment on the islands, not only for species temporarily extinct, already considered, but also for species spreading generally into the adjacent mainland from f rther away. This accounts for the relatively large proportion of species in which the northerly limit to the British breeding range is the Pentland Firth, as discussed in Part 1. Indeed, the phenomenon applies to all islands. Thus England lacks several species which breed regularly on the other side of the English Channel, and Ireland lacks a number of species which breed regularly on the other side of the Irish Sea. Such areas of sea often provide only a temporary check to the spread of a species, as shown by the many recent colonizations in Orkney, but as there are always a fairly large number of species which are spreading, there are always a relatively large number whose distribution temporarily stops at an area of sea.

### (d) *Change in bird populations*

This discussion especially demonstrates the remarkably large amount of change going on in island bird populations. Theoretical discussions on the balance of animal populations and on predator-prey relationships lead one to expect either relative stability or regular cyclic fluctuations in animal populations, the paramount mortality factors being those which proportionately increase with increasing density of the species. But this postulates a relatively stable environment, a condition which perhaps does not exist outside a laboratory culture, and certainly does not exist for most animals of the Arctic and North Temperate regions with their extremely marked differences in climate between one year and the next. Further, such theoretical conclusions could apply only to large populations. Where populations are small and isolated, any general tendencies to stabilization or regular cyclic fluctuation due to the operation of density-dependent factors will be very largely, and perhaps completely, offset by the random distribution of non-density-dependent mortality factors. In Orkney it is probably true to say that, at least in most years, ecological saturation and stability is nowhere near attainment among at least most land and fresh-water birds in at least most places.

While all these arguments particularly apply to island land birds, mainland bird populations at times exist in small, somewhat isolated 'islands', but the extent to which the phenomena considered here apply to mainland populations only future investigation can determine.

SUMMARY

1. The breeding birds of Orkney are summarized in Tables 1 and 2, and those of other British small islands in Part 2.

2. There is a progressive reduction in the number of inland species found breeding in Caithness (89), Orkney (67), Shetland (35), and Faeroes (19) respectively. Other small islands also demonstrate that, the smaller and more remote the island, the more impoverished the bird fauna compared with the mainland. This is due partly to habitat limitations, partly to the small size of many island populations and hence their liability to extinction, and partly to the sea acting as a temporary check to spreading species.

3. Distributions among islands are often erratic, due partly to local and temporary extinction of small populations, and partly to the chance manner of spread of increasing species.

4. Many, on smaller islands most, land and fresh-water species are represented by populations of under ten pairs each.

5. In Orkney over 80 % of the land and fresh-water species have markedly changed in status in the last 100 years. Similar changes have occurred on all the other islands for which there are sufficient records. In the sea birds the changes are much less marked.

6. Some increases are due to the planting of trees and bushes, to the increase of agricultural land and to protection, and a few to habitat adaptations, some decreases to the decrease of moorland, to human destruction and to periodic bad seasons.

7. Many fluctuations, especially on the smaller islands, are due to the random incidence of non-density-dependent mortality factors, which, when the total population is small, may often exterminate the whole of it.

8. Some increases and decreases have occurred on a wide scale without any obvious alteration in the environment. Possibly there has been an internal change in the species.

9. Seven cases of marked habitat change by birds are recorded, six of them in Orkney.

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# ANIMAL MORTALITY ON THREE MILES OF YORKSHIRE ROADS

By W. PICKLES

## 1. Introduction

The following paper is an attempt to show how the animal mortality fluctuates throughout the year on a stretch of country road with heavy traffic. The survey was carried out on a section of the Great North Road from Hook Moor to Aberford (1 mile) and on a section of a branch road from Hook Moor to Garforth (2 miles), the total distance being 3 miles. Although the distance was small, owing to the fact that it has been traversed twice a day on a pedal cycle, I trust that a fairly accurate record of the animal deaths has been obtained. By travelling slowly, the remains of small creatures such as insects, worms, etc., have been noted.

Previous investigators of the animals killed on roads (Barnes (**1**), Beadnell (**2**), Scott (**4**), and Hadley (**5**)) in their surveys covered much greater road-lengths and appear to have confined their observations to the vertebrates killed on the roads.

Although the lengths of road are isolated stretches, and can therefore only give a rough guide to the effects of traffic on the animal death-rate, it will, no doubt, illustrate this effect on country roads in general.

Both stretches of road are bordered for the greater part of their lengths by fields, either under cultivation or as meadows, except near Garforth (where a small housing estate is passed) and where the Great North Road enters Aberford. With these exceptions, and for a distance of a few hundred yards on one side where it is walled off from an estate, the road is bordered by hedges, chiefly by hawthorn (*Crataegus*). Both stretches of road are free from overhead wires, except for half a mile at the Garforth end, where there are electric cables. The death-rate here recorded is purely that at the road surface. That this mortality is not the absolute total, will be recognized by the fact that those which have met their end on car radiators, windscreens, etc., or died off the road itself, cannot be included.

## 2. The causes of death

(*a*) *Mammals.* All the mammals that have been found have been killed by being crushed, either completely or to such a degree that death has been rapid. I have not found a case where an injured creature has crawled to the side and died; they have all been found where they were killed.

(*b*) *Birds.* The same thing can be said about the birds; they were in most cases very badly crushed.

(*c*) *Amphibians.* The frogs that were found dead were in nearly all cases very badly crushed; though the newt found on 22 September 1938, had the ventral body wall burst, with the viscera protruding.

(*d*) *Worms.* The worms have suffered death in two ways. Some of them have been directly run over and crushed by the passing traffic; but others, having been forced out of their burrows by rain, have got on to the road, and, being unable to get back to the grass at the side, have dried up when the sun has come out, and so have died.

(*e*) *Insects.* These creatures have formed the major part of the record.

*Coleoptera.* Most of these have been the dorbeetle (*Geotrupes stercorarius*). They have been killed mostly by being crushed—the elytra often being broken off and the viscera protruding through the body wall. Some of them, however, seem not to have been directly run over, but to have been killed by the impact with the road surface caused by the currents of air behind the rapidly moving vehicles.

*Hymenoptera.* As with the Coleoptera, the Hymenoptera, chiefly bees, have met their deaths either by being crushed by the wheels of the vehicles, or in the manner indicated above. I particularly made observations on the bees and found that many of them were not completely crushed, as was the case with the ones that had been under the wheels of the vehicles, but were only punctured about the abdomen and had the gut ruptured. On many occasions I noticed that after a motor had passed by, a bee would be thrown to the side of the road, having been caught by the currents of air that follow a rapidly moving car. On examining these specimens, some were found to have punctured abdomens and some were not. To test out the idea that death was due to the impact with the road, I got a bumble-bee and threw it to the ground with considerable force. On examining it I found that its abdomen had been burst and honey was oozing out of the wound, exactly as with many specimens found on the road.

It has been mentioned above that some of the bees showed no sign of such mutilation. It seems possible that some of the bees have had an impact severe enough to cause an internally fatal wound but not sufficient to rupture the abdomen. These insects lie on their backs and go round in circles, but are unable to regain their feet and fly away. Some of them may even be only stunned and, being unable to regain their feet and crawl away, are killed by an oncoming car. That this is so is illustrated by the fact that if a bee in such a predicament is placed on the grass by the side of the road, it immediately starts to crawl about and in many cases bees have been seen to fly away. Some of these stunned and mutilated bees have been found to be dried fast to the road; this was particularly the case on 1 and 2 August 1938, which were very hot days.

*Diptera.* These insects met their deaths in the same way as the Hymenoptera; but their abdomens had not been burst open as was the case with the bees.

(*f*) *Molluscs.* The only molluscs found dead on the roads were the slugs *Agriolimax agrestis*. These were in all cases completely crushed.

### 3. Fluctuations in mortality

Tables 1 and 2 show the fluctuations of the numbers of animals found dead on the length of road under observation. Table 1 gives the figures for the Great North Road and Table 2 for the Garforth-Hook Moor Road. On both sections of road mortality has been greatest during the hot weather. Besides the effect of the temperature, there has been the effect of the rain. With Hymenoptera there was a decrease in mortality; but after rain, with the dorbeetle an increase resulted. A similar effect was caused by rain on the worms. Only once, on 12 October 1938, did the rain bring forth slugs in sufficient numbers to cause a great mortality. On that day there was a warm southerly wind and frequent showers of rain and the two things brought out a large number of slugs, and 69 were found to have been killed on the Garforth-Hook Moor Road.

August was the month having the greatest mortality, this being possibly due to the greatly increased animal population at this season of the year (Hymenoptera certainly made their contribution to this mortality). Following this there was a gradual return to the average, until the decline in numbers due to the colder weather made itself evident.

### 4. Ants and dead insects

As far as possible I have attempted to record all the dead insects on the stretches of road under observation; but there has been one error over which I have had no control. On many occasions it was noticed that there were living ants crawling about on the edge of the road foraging. They were observed to pick up dead insects, such as a hover-fly, wasp or bee, and drag them along to their nest. On several occasions I also noticed them to be busy dismembering bees in order to take the parts back to the nest. Certainly these ants have introduced an error, as the total number of insects killed on the road would include those which the ants have carried away.

I made some observations on the foraging territory of these ants from a nest in the grass on the edge of the Great North Road. I found that they keep to the gutter and crawl more or less parallel with the road, not venturing very far on to it, there being little or no food there, the bees and other insects wafted into the gutter forming a constant supply of food for them. The maximum distance travelled by these ants was 7 ft. from the nest. This is within the territory noted by me for this species of ant at Thornhill (**3**). The fact that the food is ready for them in the gutter will have tended to restrict their searches.

From this result we may conclude that these ants, living on the verge of a busy road, derive some, at least, of their food from the victims of modern road traffic and that man is providing them with a new source of food.

### 5. Effect of trees

Part of the stretch of road near Hook Moor has beech trees (*Fagus sylvatica*) overhanging the Garforth-Hook Moor section. These trees have had a marked effect on the number of animals killed on that part of this road. Only a very few were found dead there, and these were mostly mammals and birds and one wasp. This is accounted for, presumably, by the fact that the trees interrupt the current of wind which helps to blow insects along and so they rise above them and miss the traffic. This stretch of the Garforth-Hook Moor Road, about a third of a mile long, had only four deaths.

The part of the Great North Road around Hook Moor was also free from a heavy toll of animal life. As insects have formed the greatest part of the total mortality, the places of heaviest toll were the more exposed parts of both stretches of road.

### 6. Results of the survey

Several interesting points have come to light as the result of this survey.

(1) A busy road passing through a country district has a big effect on the animal life in its vicinity. The fact that dead insects are used as food by ants is one effect and has been discussed above. Besides this, it seems evident that, owing to the fact that at least one specimen of *Necrophorus humator* was found killed, these insects make their way to the road in search of the dead animals which are to be found there. In so doing they are in danger of being killed themselves; and that although they come to bury the carcasses of mammals and birds which have been killed, they are unable to do so. A country road, with fairly heavy traffic, and thus causing a considerable animal mortality, will therefore attract these insects and so reduce their numbers in that region around it.

The flies that have been killed are mostly those which might alight on horse droppings. Perhaps the reason why the number of flies has been small is because the horse traffic along the roads is very small in comparison to the motor traffic.

(2) Throughout the year 1938, the total number of animals killed on the 3 miles of road under observation was 687: 304 on the Great North Road and 383 on the Garforth-Hook Moor Road. This is 229 per mile; of which 113·3 were Hymenoptera. In Tables 1–4 the figures for each group of animals killed on the roads are given.

In Table 4 the percentage death-rate is given for each group of animals. The total number of vertebrates killed was 94 for the 3 miles of road, an average of 31·3 per mile. This is approximately the same figure as Scott's (**4**). i.e. 39·1 per mile in Iowa.

Table 1. *Number of animals killed on the Great North Road*

| Date 1938 | No. of days observation | Mammals | Birds | Amphibians | Worms | Coleoptera | Hymenoptera | Diptera | Various | Total |
|---|---|---|---|---|---|---|---|---|---|---|
| Jan. | 31 | — | 2 | — | 3 | — | — | — | — | 5 |
| Feb. | 28 | — | 2 | — | — | — | — | — | — | 2 |
| Mar. | 18 | — | 3 | — | 3 | 6 | — | 1 | — | 13 |
| Apr. | 30 | — | 3 | — | — | 4 | 14 | — | — | 21 |
| May | 31 | 1 | 2 | — | — | 3 | 28 | — | — | 34 |
| June | 21 | 1 | 1 | — | — | 1 | 10 | — | — | 13 |
| July | 21 | — | — | — | — | 2 | 13 | — | — | 15 |
| Aug. | 22 | — | 3 | — | 4 | 10 | 129 | 7 | 1 | 154 |
| Sept. | 30 | — | 5 | — | 8 | 12 | 9 | — | — | 34 |
| Oct. | 31 | 1 | — | — | 1 | — | — | — | — | 2 |
| Nov. | 30 | 1 | — | — | 8 | 1 | — | — | — | 10 |
| Dec. | 31 | — | — | — | 1 | — | — | — | — | 1 |

Table 2. *Number of animals killed on the Garforth-Hook Moor Road*

| Date 1938 | No. of days observation | Mammals | Birds | Amphibians | Worms | Coleoptera | Hymenoptera | Diptera | Various | Total |
|---|---|---|---|---|---|---|---|---|---|---|
| Jan. | 31 | — | — | — | 3 | — | — | — | — | 3 |
| Feb. | 28 | 4 | 1 | — | 2 | — | — | — | — | 7 |
| Mar. | 18 | 3 | 3 | 3 | 2 | 4 | — | — | — | 15 |
| Apr. | 30 | — | 4 | 1 | — | 5 | 17 | 3 | — | 30 |
| May | 31 | 2 | 4 | — | 3 | 5 | 18 | 1 | 1 | 34 |
| June | 21 | — | 2 | 3 | 2 | 1 | 19 | — | — | 27 |
| July | 22 | 4 | 1 | 1 | 4 | 4 | 26 | — | 1 | 41 |
| Aug. | 22 | — | 7 | 1 | 4 | 4 | 49 | 3 | — | 68 |
| Sept. | 30 | 1 | 5 | 11 | 10 | 9 | 7 | 2 | 2 | 47 |
| Oct. | 31 | — | — | 2 | 15 | 1 | 1 | — | 70 | 89 |
| Nov. | 30 | 2 | 1 | 2 | 11 | — | — | — | — | 16 |
| Dec. | 31 | — | 1 | — | 5 | — | — | — | — | 6 |

Table 3. *Total numbers of animals killed on the roads*

| Road | Mammals | Birds | Amphibians | Worms | Coleoptera | Hymenoptera | Diptera | Various | Total |
|---|---|---|---|---|---|---|---|---|---|
| Great North Road | 4 | 21 | — | 28 | 39 | 203 | 8 | 1 | 304 |
| Garforth-Hook Moor Road | 16 | 29 | 24 | 61 | 33 | 137 | 9 | 74 | 383 |
| Totals | 20 | 50 | 24 | 89 | 72 | 340 | 17 | 75 | 687 |

Table 4. *Percentage mortality of each animal group*

| Road | Mammals | Birds | Amphibians | Worms | Coleoptera | Hymenoptera | Diptera | Various |
|---|---|---|---|---|---|---|---|---|
| Great North Road | 1·3 | 6·9 | 0·0 | 9·2 | 12·8 | 66·8 | 2·6 | 0·3 |
| Garforth-Hook Moor Road | 4·1 | 7·6 | 6·3 | 15·9 | 8·6 | 35·8 | 2·3 | 19·3 |
| For the whole 3 miles | 2·9 | 7·3 | 3·5 | 12·9 | 10·5 | 49·5 | 2·5 | 10·9 |

Altogether, there were 42 different species of animals killed on the roads. These were:

MAMMALS

Sorex minutus L.
Microtus agrestis L.
Oryctolagus cuniculus L.
Talpa europoea L.
Erinaceus europoeus L.
Mustela nivalis

BIRDS

Corvus frugilegus L.
Prunella modularis Hart.
Turdus ericetorum Turton
Emberiza citrinella L.

AMPHIBIA

Rana temporaria L.
Molge vulgaris L.

INSECTS

COLEOPTERA

Geotrupes stercorarius L.
G. sylvaticus Panz.
Ocypus olens Müll.
Harpalus rufipes Deg.
Aphodius fimetarius L.
Carabus problematicus Hbst.
C. monilis F.
Necrophorus humator Gze.
Feronia madida F.

HYMENOPTERA

Bombus terrestris L.
B. lapidarius L.
B. muscorum L.
B. agrorum F.
B. ruderatus F.
Apis mellifera L.
Colletes succinata L.
Andrena armata Gmel.
Vespula vulgaris L.
V. germanica F.

DIPTERA

Tipula oleracea L.
Syrphus ribesii L.
S. luniger Mg.
Eristalis tenax L.
Sarcophaga carnaria L.
Calliphora erythrocephala Mg.
Dasyphora cyanella Mg.
Mesembrina meridiana L.

LEPIDOPTERA

Triphoena pronuba L.

MOLLUSCA

Agriolimax agrestis L.

OLIGOCHAETA

Lumbricus terrestris L.

Not a single reptile was killed, though there are lizards to be found on Hook Moor. Snakes are not by any means common.

From this survey, therefore, it seems that a busy road passing through a country district is a definite factor to be reckoned with, and its effect on the animal life in the immediate vicinity cannot be ignored. It acts indiscriminately, killing useful as well as harmful creatures, and it may also be counted as a factor in the survival of these animals.

## 7. Acknowledgements

I wish to thank the following experts at the Natural History Museum, London, for kindly identifying specimens: Mr G. I. Crawford (Mollusca), Dr K. G. Blair (Coleoptera, Diptera and Lepidoptera), and Mr Charles Elton for valuable criticism and assistance.

## 8. Summary

1. An attempt has been made to record the mortality caused by modern traffic on a 3-mile stretch of road between Garforth and Aberford during the year 1938.

2. *Causes of death.* Besides being directly run over, many insects, the various bees mentioned in particular, are killed by being thrown on to the road and fatal injuries are caused.

3. *Fluctuations in mortality.* Naturally the numbers of deaths increased towards the summer months, August showing the peak of deaths. This is also the period of greatest traffic and the peak of animal life. The greatest mortality occurred during the hottest week of the year.

4. *Ants and dead insects.* It was found that specimens of the ant, *Myrmica ruginodis*, living in the grass verge of the Great North Road went about picking up dead bees, etc., and dragged them back to the nest for food. Here, then, was a source of food for these ants.

5. *Trees.* The trees round about Hook Moor caused the sections of the Great North Road and the Garforth-Hook Moor Road over which they hung to be nearly free from casualties.

6. *General.* A busy road is a cause of death to the inhabitants of its immediate vicinity, and as such it may be of survival value, as the weakest will be killed being unable to get away from the traffic. Besides this the horse droppings and the dead carcasses attract insects (flies and *Necrophorus* for instance) which would normally only come accidentally to the spot.

In the 3 miles of road a total of 687 creatures was killed covering 42 species of animals. This works out at 229 creatures per mile.

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# THE RAT AND MOUSE POPULATIONS OF CORN RICKS

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(*With Plate* 1 *and* 3 *Figures in the Text*)

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## 1. Introduction

In September 1939 the Bureau of Animal Population, under the auspices of the Agricultural Research Council, began research into methods of controlling brown rats (*Rattus norvegicus*) and house-mice (*Mus musculus*) in and around farms and, among other problems, studied that of protecting corn ricks or clearing them of rodent infestations. It soon became apparent, however, that almost nothing was known of these populations and that it was necessary to find out a great deal more about their biology, and population dynamics. Without this knowledge a scientific approach to methods of control was impossible.

Corn ricks were found to be a habitat of major importance for farm rats and mice. In many cases it was found from local surveys undertaken by members of the Bureau that numbers were living in the ricks by midwinter and that they were doing a great deal of damage to the grain. This aggregation, however, meant that a considerable proportion of the farm infestation could be killed at threshing if the ricks were threshed before the spring exodus (from the end of April onwards) to other, scattered, parts of the farm occurred. Corn ricks, also, were found to be the main winter breeding areas, this again stressing the economic importance of such populations.

The threshing season begins as soon as the corn is fit to carry. The threshing tackle is in the cornfield, no rick being built: but the waggons unloading straight to the feeder on the drum. The straw is ricked, trussed, baled or cut

into chaff. In a wet autumn this method is uncommon because then the corn usually has to be ricked to complete its drying. Next, ricks are threshed which may have been built a few weeks or even a few days previously, as the farmer could not get the tackle immediately and did not trust the weather. There are a few Combine Harvesters in the area studied and, where these are used, there is of course not much building of corn ricks.

Around the latter part of September and in October the seed corn and most of the barley are threshed, the former for planting (wheat and winter oats) and the latter for selling to the maltsters. At this period each tackle can give only a few days to each farm (it being uneconomic to have many tackles in one district). These ricks, on all the farms, have to be threshed out early, and probably by then, also, the farmer is short of 'tail'[1] and of straw. Having completed this first round, the tackles then revisit the farms to thresh some or all of the remaining ricks. In the 1940–1 season most of the farms had all their ricks finished on this second visit, but before the control in the price of wheat and oats, many farmers kept a few ricks up far into the summer (having nowhere else to store the grain) hoping for a rise in price. These late ricks almost always became badly infested with rats and mice, and several farmers have stated that the damage to the grain counteracted the better price obtained, while, if the price did not rise much for some reason or other, they were actually out of pocket.

Before 'The Rats Order (No. 2), 1940' (issued 21 August 1940) rat killing at threshing was a casual affair, depending on the initiative of the individual farmer: the opportunity for greatly reducing the farm infestation was frequently lost. This Order says that every person using agricultural land for the purpose of threshing corn shall, before threshing, '...cause such rick to be completely surrounded by a fence not less than thirty inches high constructed of material sufficiently impenetrable by rats escaping from the rick to enable them to be killed inside the fence. If the material is wire netting, the mesh of the wire shall not be greater than one half of an inch....The fence shall be placed not less than six feet distant from the base of the rick (except on that side of the rick on which the threshing tackle is placed, on which side the distance shall be not less than three feet) and shall be secured to the ground in such manner as to prevent rats from passing underneath it. The fence shall be maintained in position continuously until the threshing of the rick is completed. The space between the fence and the base of the rick shall at all times be kept clear of corn, thatch, straw or other obstructions which may afford cover or protection for rats. Every person who occupies such land shall take effective steps to destroy rats escaping from any rick.'

This was followed on 8 August 1941 by 'The Rats Order, 1941', which placed the responsibility of erecting the fence and killing the rats jointly on

[1] Rodent-damaged grain, and weed seeds, which have been automatically sieved out, often used for poultry feeding.

to the owner of the rick, the owner of the land and those in charge of the threshing operations. It is still legal to allow the mice to escape.

These Orders apply only to England and Wales. Although no general Order of the kind has been issued in Scotland, local Orders on very similar lines are operated in a large number of counties.

## 2. Methods of collecting data

During the threshing season of 1939–40, only farms known to be rat-infested were visited by the Bureau of Animal Population or had rats and data obtained from them. In the threshing season of 1940–1 three reliable Oxfordshire and Berkshire threshing tackle foremen co-operated; one from Wilder's of Wallingford, one from Thatcher's of Abingdon and one from Curtis's of Oxford. The complete data from every rick (excluding seed clover) were sent in, together with most of the dead rats, and these, with the ricks from the Agricultural Research Council's field station at Compton, Berkshire, and some places visited by L. S. V. V., may be said to sample a fair cross-section of corn ricks in the district round Oxford.[1] In the first season's work L. S. V. V. was present at the threshing of 45 of the ricks, but in the second season the majority of the field data were sent in by the foremen unaided except for occasional visits.

The questions answered were as follows:

(1) Farmer's name and address.
(2) Kind of grain.
(3) Built on staddles, faggots, rakings or straw.
(4) In field or yard.
(5) Number of rats in rick.
(6) Number of mice in rick.
(7) Number of rat nests and number of young per nest.
(8) Number of mouse nests and number of young per nest.
(9) Date(s) built.
(10) Date(s) threshed.
(11) Remarks on damage to grain.
(12) Single rick or one of a group? If latter—grouped with which ricks?

During the season of 1940–1 the foremen were paid 1*s*. per rick irrespective of whether it contained rodents or not, so there was no temptation to add to the numbers, as frequently happens with the bounty system.

Question 2 is discussed on p. 65. Question 3 will not be used in future as no ricks in these rounds are built on staddles, and whether the rick is on a straw or faggot foundation seems to have no influence on the rodent population. Question 4: these data are still being collected, but are not being discussed in the present communication. Question 6 is, of necessity, an esti-

[1] The general physical and agricultural environment in this region has been described in the *Victoria County History of Oxford*, and the *Land Utilization Survey Report on Berkshire* ('The land of Britain', Part 78, 1936).

mate—and usually an overestimate. As L. S. V. V. has frequently been threshing with all three foremen, however, he knows roughly by how much they overestimate. This applies to Question 8 too.

Questions 5 and 7 are much more accurate, as the rats are killed and collected or, if any escape, they are usually seen to do so. Question 5 refers only to 'active' rats, i.e. those not found actually in or crawling away from the nest. Rats arouse the 'sporting instinct' of both the men and the dogs at the rick; but mice, being small, are frequently allowed to escape and colonize other ricks or parts of the farm. Most of the ricks were surrounded with wire-netting 2–3 ft. high during threshing, at a distance of about 3 yd. from the rick, except on the side nearest the drum, to prevent rats jumping off

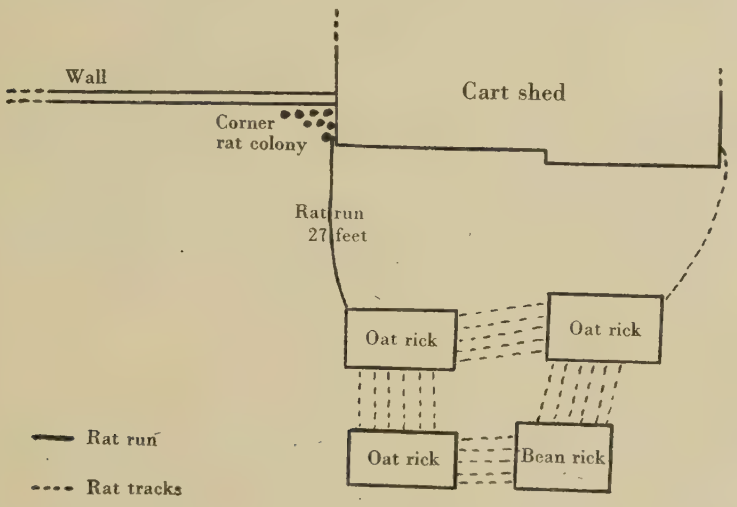


Fig. 1. Locality 125. 3 February 1940. Rickyard rat movements shown by tracks in snow. Rat colony in usual untidy nettle corner. Well-beaten run from there to the rick group. Many scattered tracks going from rick to rick. The latter were found with other rick groups visited after snowfalls and, in a few cases, a similar track was found going to a corner colony.

the rick over the wire; but it depended on the individuals whether the wire was kept free from a bank or loose straw, affording a runway over the top. Three-eighths inch mesh was found to be small enough to hold the mice, except those only out of the nest for a short time; but mostly the wire used was larger than this owing to the difficulty of supply, and many of the mice escaped.

The results of Question 11 have all been tabulated but are too unreliable to be worth obtaining in future.

Question 12 is of great importance, as ricks in a group are built close together and rats can run from rick to rick. In the vast majority of cases in the area studied, ricks in groups were merely a few yards apart so that two could be threshed without moving the drum. The group of four ricks on Fig. 1 is typical.

When L. S. V. V. was present at threshing more details were obtained, including measurements of rick and the grain yield. These are not worth continuing in the future as crops vary so much, even from one part of a given field to the other and, in any case, the foremen cannot give accurate measurements of the rick from which the bulk can be worked out, owing to such difficulties as the angles of the slopes of the sides of the roof, etc. The surroundings of the rick were also described with the nearest hedge, ditch or bank capable of harbouring rats, and the nearest buildings. This will be added to the foremen's question sheet in future. The importance of the proximity of water has been exaggerated, however, as we have records of badly infested ricks remote from any supply. In several cases the rats were known to be drinking rain and dew from the thatch, and in two cases to be grazing the green shoots of an adjacent barley crop. Mice appear to be able to do without a direct supply of water for considerable periods.

### 3. Methods of grouping data

In 1939 the first rick which was recorded was threshed on 14 November, and it seemed desirable to adopt some method of subdividing the year into time periods, which would indicate the date at which a rick group was threshed and also roughly the length of time it had been standing. Out of 87 ricks threshed during the season of 1939–40 and for which there were reasonably accurate records of the date of building, it appeared that 74 (some 85 %) had been built between 20 August and 16 September 1939. For the first season's results, therefore, the year was divided into 4-week periods beginning on 12 November 1939, and it followed that any rick group which was threshed, for example, between 12 November and 9 December 1939 had been standing on the average for some 12 weeks.

The same grouping was retained during the second year in order that the first two or any subsequent season's results might be comparable as regards threshing dates. Owing, however, to the excellent harvest conditions which operated during 1940, the ricks were built earlier than in 1939. Out of 250 ricks which were threshed before 2 April 1941 the following dates of building were recorded:

| 1940 week | No. of ricks |
|---|---|
| 30 July–5 Aug. | 3 |
| 6–12 Aug. | 49 |
| 13–19 Aug. | 104 |
| 20–26 Aug. | 51 |
| 27 Aug.–2 Sept. | 6 |
| 3–9 Sept. | 9 |
| 10–16 Sept. | 19 |
| 17–23 Sept. | 9 |
| | 250 |

The second mode in this distribution represents, for the most part, barley ricks which as a general rule are cut, carried and stacked later than either oats or wheat. There also exist, of course, local differences (depending on soil,

*Photo C. Elton*

Photo 1. Rat run up side of barley rick, from burrow in base to thatch (November 1941).

*Photo A. D. Middleton*

Photo 2. Rat burrows in base of wheat rick (November 1941).

*Face page* 48

climate, etc.) between the dates at which the same crop can be stacked. Taking the distribution as a whole, the modal week appears to be 13–19 August. Roughly on the average, therefore, ricks during the harvest of 1940 were built some $2\frac{1}{2}$ weeks earlier than in 1939. In comparing any ricks threshed between two particular dates during the first season with those threshed between the same dates during the second, it must be remembered that the latter had been standing about a fortnight longer than the former.

### 4. Number of ricks recorded

During the first season (1939–40) only those ricks having a moderate or heavy degree of rat infestation were recorded, while during the second season a more complete survey was undertaken of all ricks which were threshed by three contractors' tackles and by the tackle at the Agricultural Research Council's field station at Compton.

For reasons which have already been given (see Fig. 1) it was decided to take as a unit the rick group and not the individual rick. A rick group may consist of anything between 1 and 6 ricks, and the frequency of rick groups formed by 1, 2, 3, 4, 5 and 6 individual ricks during the two seasons' work are given in Table 1. It will be seen that during 1939–40 a total of 45 rick groups formed by 99 ricks was recorded, and during 1940–1 221 rick groups (419 ricks), making a grand total for the two seasons of 266 rick groups and 518 ricks. The average number of ricks per rick group was 2·21 for the first season and 1·90 for the second. In addition, there were a number of incomplete records for rick groups threshed during 1939–40, but these are not considered in the present analysis (for distribution of all ricks see Fig. 2).

In regard to the second season's threshing two small points might be noted. The first rick group recorded was threshed on 9 and 10 August 1940 and the last on 23 and 24 July 1941. In grouping the ricks in 4-week periods these two rick groups were included with those falling in the periods 20 August–16 September and 25 June–22 July respectively.

### 5. Degree of infestation with rats and mice

The reports received in the laboratory recorded the number of active rats killed and seen escaping, together with the number of nests. Since the number of nestlings found in the latter might or might not be accurately recorded in some instances, it was assumed throughout that a nest contained on the average 7 young, a figure which has been shown to be substantially correct by personal counts at a number of ricks during threshing. Thus during the first season 85 complete nests were found to contain a total of 621 young, an average of 7·31 per nest. The greatest number of young in any one nest was 13 and the smallest 3. Another series of records was derived from single nests which were examined in the laboratory and of which some had already been entered in the field records; but there were also included a number for which

Table 1. *Number of ricks recorded*

| No. of ricks in group | Rick groups threshed during: 20 Aug. to 16 Sept. | 17 Sept. to 14 Oct. | 15 Oct. to 11 Nov. | 12 Nov. to 9 Dec. | 10 Dec. to 7 Jan. | 8 Jan. to 4 Feb. | 5 Feb. to 4 Mar. | 5 Mar. to 1 Apr. | 2 Apr. to 29 Apr. | 30 Apr. to 27 May | 28 May to 24 June | 25 June to 22 July | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1939–40 | | | | | | | | | | | | | |
| 1 | — | — | — | 2 | 2 | — | 5 | 2 | 3 | 2 | — | 2 | 18 |
| 2 | — | — | — | 1 | 1 | 2 | 3 | 1 | 3 | 2 | 1 | 1 | 15 |
| 3 | — | — | — | — | 1 | — | — | — | 1 | — | — | — | 2 |
| 4 | — | — | — | 1 | 3 | — | 1 | — | — | — | 1 | — | 6 |
| 5 | — | — | — | 1 | — | — | — | — | — | 2 | — | — | 3 |
| 6 | — | — | — | — | — | — | — | 1 | — | — | — | — | 1 |
| Total | — | — | — | 5 | 7 | 2 | 9 | 4 | 7 | 6 | 2 | 3 | 45 |
| | | | | | | | | | | | Total no. of ricks | | 99 |
| 1940–1 | | | | | | | | | | | | | |
| 1 | 11 | 11 | 21 | 11 | 12 | 8 | 13 | 8 | 7 | 5 | 2 | 1 | 110 |
| 2 | 1 | 7 | 8 | 6 | 8 | 5 | 7 | 6 | 1 | 2 | — | 2 | 53 |
| 3 | 2 | 9 | 3 | 6 | 4 | 4 | 3 | 5 | — | 1 | — | — | 37 |
| 4 | 1 | 1 | 3 | 1 | 2 | 1 | 2 | 2 | — | 1 | — | — | 14 |
| 5 | — | 2 | 1 | — | — | 1 | 1 | — | 1 | — | — | — | 6 |
| 6 | — | — | — | — | 1 | — | — | — | — | — | — | — | 1 |
| Total | 15 | 30 | 36 | 24 | 27 | 19 | 26 | 21 | 9 | 9 | 2 | 3 | 221 |
| | | | | | | | | | | | Total no. of ricks | | 419 |

Fig. 2. Map showing the distribution of corn ricks, the threshing data of which were obtained by the Bureau of Animal Population. Upper figure denotes number of ricks obtained during season 1939–40: lower figure number obtained season 1940–1. The figures mark the approximate position of the villages.

Not included: Barford, Warwick ... 8
2

Membury, Wilts ... 6
0

no field count had been made, each nest merely having been put into a single container and sent into the laboratory. The 64 complete nests thus examined contained a total of 429 young, an average of 6·70 per nest.

Similar records for the numbers of 'active' individuals and nests were made for house-mice, but in this case there is every reason to suppose a much greater degree of inaccuracy. The figures for the number of mouse nests observed are very doubtful, and may be very much on the low side owing to the tendency for these to be built within the sheaves. The assessment of the number of mice must be regarded as highly approximate as compared with the number of rats. In the great majority of cases the three threshing-tackle foremen sent in a numerical estimate of the number of mice. Sometimes, however, and frequently with threshing data obtained from other sources, they were described as 'many', 'few', etc. The following table has been used throughout in the analysis of corn-rick mouse populations and is based on personal contacts with the men and knowledge of their ideas on what does in fact constitute 'many' mice or 'about a hundred' mice. In a number of cases L. S. V. V. was present right through the threshing of a rick and, having killed and counted all the mice, would ask the foremen how many there had been. Two of the foremen slightly overestimate in high populations and the third always much overestimates save in very low populations. Their errors are always pretty constant, so a fair degree of accuracy (but nothing more) is claimed for the following orders of infestation:

| Class | Approx. no. of active mice per rick | Degree of infestation |
|---|---|---|
| 0 | No mice seen | |
| 1 | 1– 19 | Few |
| 2 | 20– 49 | Fair number |
| 3 | 50– 99 | Many |
| 4 | 100–199 | Very many |
| 5 | Over 200 | Too numerous to estimate |

The results of this system of classification are given in Table 3.

In the case of the rat figures a higher degree of accuracy was undoubtedly obtained, and in Table 2 the rick groups are tabulated according to the *total* population of rats of all ages reported in them, allowing an average of 7 young per nest. Thus for each 4-week period the number of rick groups reporting no rats, under 5 rats, 5–9, 10–19, etc., are given, the group limits for the size of the rat population increasing geometrically for populations of 5 rats and over.

*Number of rick groups reporting absence of rats or mice or both*

For the reasons which have already been given it has been impossible to assess this figure for the first season's threshing. For 1940–1, when the sampling of ricks was complete (in so far as the experience of three threshing-tackle firms went), the proportion of negative rick groups for rats and mice is given in Tables 2 and 3. As is quite natural, those rick groups which were

Table 2. *Frequency distributions of the total number of rats (all ages) reported in each recorded rick group*

| Total no. of rats in rick group | No. of rick groups threshed during: 20 Aug. to 16 Sept. | 17 Sept. to 14 Oct. | 15 Oct. to 11 Nov. | 12 Nov. to 9 Dec. | 10 Dec. to 7 Jan. | 8 Jan. to 4 Feb. | 5 Feb. to 4 Mar. | 5 Mar. to 1 Apr. | 2 Apr. to 29 Apr. | 30 Apr. to 27 May | 28 May to 24 June | 25 June to 22 July |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | 1939–40 | | | | | | |
| 0 | — | — | — | — | — | — | — | — | 1 | — | 1 | — |
| 1–4 | — | — | — | — | — | — | — | 1 | — | — | — | — |
| 5– | — | — | — | 1 | — | — | — | — | — | — | — | — |
| 10– | — | — | — | 2 | 1 | — | 1 | — | 1 | — | — | 1 |
| 20– | — | — | — | — | 2 | 2 | 3 | — | 1 | — | — | — |
| 40– | — | — | — | 2 | 1 | — | 1 | 2 | 1 | 1 | 1 | 1 |
| 80– | — | — | — | — | 3 | — | 3 | — | 1 | 4 | — | — |
| 160– | — | — | — | — | — | — | 1 | — | 1 | 1 | — | 1 |
| 320– | — | — | — | — | — | — | — | 1 | 1 | — | — | — |
| 640– | — | — | — | — | — | — | — | — | — | — | — | — |
| Total no. of rick groups | — | — | — | 5 | 7 | 2 | 9 | 4 | 7 | 6 | 2 | 3 |
| | | | | | | 1940–1 | | | | | | |
| 0 | 15 | 29 | 30 | 16 | 13 | 10 | 10 | 10 | 1 | 5 | — | — |
| 1–4 | — | 1 | 1 | 5 | 3 | 3 | 3 | 4 | 1 | — | — | — |
| 5– | — | — | 3 | — | 4 | 2 | 5 | 2 | 1 | 2 | — | — |
| 10– | — | — | 1 | 1 | 4 | 2 | 6 | 2 | 1 | — | — | 1 |
| 20– | — | — | 1 | 1 | — | 1 | 1 | 1 | 1 | — | 1 | — |
| 40– | — | — | — | — | 2 | 1 | 1 | 1 | 2 | — | 1 | 1 |
| 80– | — | — | — | — | 1 | — | — | 1 | 1 | 2 | — | 1 |
| 160– | — | — | — | — | — | — | — | — | 1 | — | — | — |
| 320– | — | — | — | — | — | — | — | — | — | — | — | — |
| 640– | — | — | — | — | — | — | — | — | — | — | — | — |
| Total no. of rick groups | 15 | 30 | 36 | 23 | 27 | 19 | 26 | 21 | 9 | 9 | 2 | 3 |
| Unoccupied rick groups % | 100 | 96·7 | 83·3 | 69·6 | 48·1 | 52·6 | 38·5 | 47·6 | 33·3 | | 0 | |

threshed very shortly after they had been built, e.g. during the period 20 August–16 September, reported a complete absence of both rats and mice. After 17 September the percentage falls until, during 5 February–4 March, 38·5 % of rick groups were unoccupied by rats and 30·8 % by mice. Generally speaking the proportion of rick groups reporting no mice is throughout lower than those reporting no rats. Both curves, however, follow a very similar course.

The percentage of rick groups in 1940–1 reporting an absence of both rats and mice is given at the bottom of Table 3, and it will be seen that by March 1941 only about 15 % of rick groups were completely free from rodent infestation.

These figures support the common-sense view that the longer a rick group is standing before being threshed the more likely it is to be occupied by either rats or mice, or both species together. They also suggest that during 1940–1 the colonization of the ricks was a gradual affair extending throughout the winter. From all accounts the degree of infestation of rats was on the light side, and a more abrupt fall in the percentage of negative rick groups might be expected in a season where the degree of infestation was heavier.

### 6. Density of rat populations according to the time the ricks were threshed

From Table 2 it appears that the total population of rats in each rick group tends, in both seasons, to increase until about April the longer the rick group remains standing, as is shown by the spread of the distributions into the larger population classes. In order to show this point more clearly Table 4 was constructed.

This table shows in columns 2 and 3 the density of active rats and of nests per rick in each rick group. As will be seen in columns 1 and 2 the variation in density per rick in different rick groups threshed during the same 4-week period is quite considerable, representing, in part at least, the known widely varying degrees of rat infestation in different localities.

During 1939–40 the mean numbers of active rats per rick, of nests and of total population follow a very similar course, rising to maximum in April and thereafter falling off somewhat.

During 1940–1 the mean values for the early periods are somewhat irregular, but again there appears to be a maximum in April. The mean total population per rick is, however, still relatively high during 28 May–22 July (the figures for 30 April–27 May are unfortunately few in number). Both active rats and nests are much lower than for the corresponding periods in the first season. However, a direct comparison in this way is hardly a fair one, since only moderately or heavily infested ricks were sampled during 1939–40.

Table 3. *Frequency distributions of estimated house-mouse populations per rick reported in each recorded rick group*

| Size of mouse population group | 20 Aug. to 16 Sept. | 17 Sept. to 14 Oct. | 15 Oct. to 11 Nov. | 12 Nov. to 9 Dec. | 10 Dec. to 7 Jan. | 8 Jan. to 4 Feb. | 5 Feb. to 4 Mar. | 5 Mar. to 1 Apr. | 2 Apr. to 29 Apr. | 30 Apr. to 27 May | 28 May to 24 June | 25 June to 22 July |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | 1939–40 | | | | | | | |
| 0 | — | — | — | — | 1 | — | 1 | 1 | — | — | — | — |
| 1 | — | — | — | 2 | 3 | 1 | 2 | 1 | 2 | 1 | — | 1 |
| 2 | — | — | — | 1 | 1 | 1 | 3 | — | 1 | 1 | 1 | — |
| 3 | — | — | — | — | — | — | 1 | 2 | 3 | 1 | — | 1 |
| 4 | — | — | — | — | — | — | 2 | — | 1 | 2 | — | — |
| 5 | — | — | — | — | — | — | — | — | — | 1 | 1 | 1 |
| Total no. of rick groups | — | — | — | 3 | 5 | 2 | 9 | 4 | 7 | 6 | 2 | 3 |
| | | | | | 1940–1 | | | | | | | |
| 0 | 15 | 23 | 23 | 13 | 14 | 7 | 8 | 4 | 2 | 3 | 1 | 1 |
| 1 | — | 2 | 3 | 5 | 6 | 3 | 6 | 5 | 2 | 1 | — | 1 |
| 2 | — | 2 | 4 | 4 | 1 | — | 2 | 4 | — | 1 | 1 | — |
| 3 | — | 1 | 3 | 2 | 3 | 5 | 3 | 5 | 1 | 1 | — | — |
| 4 | — | — | 2 | — | 2 | 4 | 5 | 3 | 1 | 3 | — | 1 |
| 5 | — | 2 | 1 | — | 1 | — | 2 | — | 1 | — | — | — |
| Total no. of rick groups | 15 | 30 | 36 | 24 | 27 | 19 | 26 | 21 | 7 | 9 | 2 | 3 |
| Unoccupied rick groups % | 100 | 76·7 | 63·9 | 54·2 | 51·9 | 36·8 | 30·8 | 19·0 | 31·2 | | 40·0 | |
| No. of rick groups reporting absence of *both* rats and mice | 15/15 | 22/30 | 22/36 | 9/24* | 9/27 | 4/19 | 4/26 | 3/21 | 0/7 | 3/9 | 0/2 | 0/3 |
| Ditto % | 100 | 73·3 | 61·1 | 37·5 | 33·3 | 21·1 | 15·4 | 14·3 | 18·7 | | 0 | |

* During this period one rick group was threshed at a farm where some rat experiments were in progress. Although some rats were found in this group, their numbers could not be included in Table 2.

Table 4. *Density of rats per rick in all occupied rick groups recorded*

| | No. active rats per rick | No. nests per rick | No. of rick groups | Mean no. active rats per rick | Mean no. nests | Mean total population per rick |
|---|---|---|---|---|---|---|
| 1939–40 | | | | | | |
| 12 Nov.– 9 Dec. | 2, 4, 10, 14, 52 | 0, 0·5, 0, ?, ? | 5 | 16·4 | 0·17 | 17·6 |
| 10 Dec. – 4 Feb. | 5, 10, 10, 12, 13, 28, 30, 32, 70 | 0, ?, 0, 0·5, 0, 0·3, 0, 0, ? | 9 | 23·3 | 0·11 | 24·1 |
| 5 Feb. – 4 Mar. | 6, 11, 16, 17, 25, 30, 36, 56, 160 | 2, 1·7, 0, 2, 0·5, 0, 2, 0, 0 | 9 | 39·7 | 0·91 | 46·1 |
| 5 Mar. – 1 Apr. | 1, 40, 53, 72 | 0, 4, 1, 4·7 | 4 | 41·5 | 2·42 | 58·4 |
| 2 Apr. –29 Apr. | 5, 30, 33, 35, 40, 198 | 0, 0, 8, ?, 0, 7·5 | 6 | 56·8 | 3·10 | 78·5 |
| 30 Apr. –27 May | 11, 15, 40, 47, 73, 90 | 0·5, 1·9, 1, 2·5, 6, 10 | 6 | 46·0 | 3·65 | 71·6 |
| 28 May –22 July | 3, 25, 26, 58 | 1, 0·5, 2, 4·5 | 4 | 28·0 | 2·00 | 42·0 |
| 1940–1 | | | | | | |
| 17 Sept.–11 Nov. | 0·25, 1·2, 1·7, 3, 4, 6, 8·5 | 0, 0, 0, 0·25, 0, ?, 0·5 | 7 | 3·5 | 0·13 | 4·4 |
| 12 Nov.– 9 Dec. | 0·3, 0·3, 0·5, 0·5, 1, 6, 6 | 0, 0, 0, 0, 0, 2, 0 | 7 | 2·1 | 0·29 | 4·1 |
| 10 Dec. – 7 Jan. | 0·5, 1, 3, 3, 3·3, 4·5, 5, 6, 6·5, 6·7, 8, 14·5, 16 | 0, 0, 0, 0, 0·33, 0, 0, 0, 0, 0, 0, 2, 0 | 13 | 6·0 | 0·18 | 9·2 |
| | 34·5 | | | | | |
| 8 Jan. – 4 Feb. | 0·25, 1, 3, 4·7, 5, 5, 7, 20, 46 | 0, 0, 0, 0, 0, 0, 0, 0, 1 | 1 | | | |
| 5 Feb. – 4 Mar. | 1, 1, 1·3, 2, 3, 4, 4, 6, 6, 7, 8, 8·5, 10, 17, 20, 21·5 | 0, 0, 0·33, 1, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 1·5 | 9 | 10·2 | 0·11 | 11·0 |
| 5 Mar. – 1 Apr. | 0·5, 1, 1, 1·5, 2, 4, 4·3, 7·3, 10, 20, 60 | 0, 0, 1, 0, 0, 0, 0, 0·25, 0, 1, 1 | 16 | 7·5 | 0·18 | 8·8 |
| 2 Apr. –29 Apr. | 2, 4, 4, 5, 29·6, 32, 155 | 0, 2, 3, 0, 0, 1, 3 | 11 | 10·1 | 0·29 | 12·1 |
| | 65 | | 7 | 33·1 | 1·28 | 44·9 |
| 30 Apr. –27 May | 5, 5, 14, 28·7 | 0, 0, 1, 0 | 1 | | | |
| 28 May –22 July | 3·5, 24, 38, 38, 49 | 0·5, 1, 1, 1·5, 0 | 4 | 13·2 | 0·25 | 14·9 |
| | | | 5 | 30·5 | 0·80 | 36·1 |

Total populations estimated on the basis of 7 young per nest.

In the periods 10 Dec.–7 Jan. and 2 Apr.–29 Apr. in the second season, the records from two rick groups gave only the total population of rats and were not divided into 'active rats' and nest. These are entered below the bracket in each of these time periods.

The figures for the number of nests per rick are set out in the same order as the number of active rats per rick, so that the ordinal number in each series refers to the same rick group.

### 7. Fertility of rats killed at threshing

During both seasons a large number of the rats killed at threshing time were examined in the laboratory and samples were also received from habitats other than corn ricks, e.g. country refuse dumps, hedges, banks, farm buildings, etc. It is hoped that a full account of this laboratory investigation, which was carried out in conjunction with Miss U. M. Wykes, will be published in due course, but in the meantime a short account of the degree of fertility observed among females coming from both the rick and non-rick environments is of some interest.

The degree of fertility among the females is measured by the percentage of adults visibly pregnant; and as a criterion of adultness a body weight of 115 g. was adopted. This level was determined by relating the proportion of females recorded as having copora lutea in the ovaries to body weight. In addition, it was found necessary to standardize the percentage of adult females found to be pregnant in any one time period, since the pregnancy rate was observed to depend on the weight distribution of the sample. On the whole, the heavier females tended to be more frequently pregnant than the lighter, and at the same time had a greater average number of embryos per pregnant female.

To eliminate the effect of varying weight distribution on the crude percentage of adult females pregnant, the standardized percentage was estimated in each time period by the indirect method. Between 12 November 1939 and 16 September 1941 a total of 1747 adult females coming from both the rick and the non-rick environments was examined. Their weight distribution was as follows:

| Weight group | No. females examined | No. found pregnant | Proportion pregnant |
|---|---|---|---|
| 115 – | 377 | 34 | 0·0902 |
| 195 – | 503 | 148 | 0·2942 |
| 295 – | 533 | 168 | 0·3152 |
| 395 – | 279 | 76 | 0·2724 |
| 495 + | 55 | 20 | 0·3636 |
| Total | 1747 | 446 | 0·2553 |

The average percentage pregnant determined from the totals was 25·53, and the weight-specific pregnancy rates are given in the last column. By applying these latter rates to the number of females examined in each weight group during any one particular time period, the 'expected' number of pregnant females was obtained. The ratio 'observed total number of females pregnant'/'expected total number of females pregnant' multiplied by 25·53 then gives the standardized percentage for that time period.

These figures are given in Table 5, together with the number of females examined. The course of events in both seasons shows certain similarities. During the first season (1939–40) between 12 November and 4 March the

percentage of females pregnant in the rick populations was high (25–28), whereas in the non-rick environment it was low, being just over 3 % during 12 November–4 February and zero between 5 February and 4 March. These differences were found to be statistically significant using the $\chi^2$ test. After 4 March there was a rise, which was marked in the non-rick environment, to a peak in April, when some 40 % of the rick and 49 % of the non-rick females were pregnant, and no significant difference could be established between the environments. After the end of April there was a fall in both series, and during the period 23 July–16 September, a season when there were no rats in the few ricks which were threshed, only some 9 % of the non-rick females were pregnant as compared with 49 % during April.

In the second season (1940–1) the winter difference between the environments was again established, and during 12 November–7 January the percentages were 24 in the rick and 3 in the non-rick females respectively. During

Table 5. *Standardized percentage of adult female rats found to be pregnant*

| | 1939–40 | | | | | | 1940–1 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Rick | | | Non-rick | | | Rick | | | Non-rick | | |
| | *N* | *P* | % | *N* | *P* | % | *N* | *P* | % | *N* | *P* | % |
| 17 Sept.–11 Nov. | — | — | — | — | — | — | 21 | 7 | 32·26 | 41 | 6 | 13·16 |
| 12 Nov.– 7 Jan. | 70 | 20 | 27·84 | 172 | 6 | 3·26 | 82 | 18 | 23·60 | 35 | 1 | 2·68 |
| 8 Jan. – 4 Feb. | | | | | | | 42 | 4 | 10·73 | 9 | 0 | 0·00 |
| 5 Feb. – 4 Mar. | 258 | 63 | 24·95 | 20 | 0 | 0·00 | 54 | 14 | 29·01 | 28 | 3 | 11·12 |
| 5 Mar. – 1 Apr. | 168 | 59 | 34·55 | 35 | 7 | 18·12 | 55 | 23 | 38·94 | 24 | 2 | 7·37 |
| 2 Apr. –29 Apr. | 87 | 32 | 39·87 | 48 | 27 | 48·75 | 127 | 62 | 55·97 | 19 | 5 | 24·36 |
| 30 Apr. –27 May | 121 | 42 | 37·94 | 7 | 2 | 35·96 | 54 | 22 | 39·61 | 10 | 1 | 9·12 |
| 28 May –22 July | 36 | 2 | 5·64 | 14 | 3 | 18·82 | 35 | 7 | 19·09 | | | |
| 23 July –16 Sept. | 0 | — | — | 56 | 6 | 9·41 | 0 | — | — | 19 | 2 | 11·82 |

*N* = number of adult females (>115 g.) examined.
*P* = number of adult females (>115 g.) found pregnant.

8 January–4 February there was a fall to 11 % in the ricks, afterwards rising to a peak again in April, when some 56 % were pregnant. In a similar way to the first season the percentage again fell away to 19 % pregnant during 28 May–22 July. The non-rick figures during the second season were somewhat irregular, but again there is a suggestion of a peak in April followed by a fall. During 23 July–16 September the percentage was 11·8, a figure very similar to that of 9·4 % observed at the same time of year during the first season.

The principal point which emerges from this table, and the importance of which we wish to stress at the present moment, is the differences in fertility which were found during the winter months (say between November and March) between the females killed in the ricks and those killed outside. Whereas the rick female is in both seasons breeding at a relatively high rate as judged from the proportion of them found to be pregnant, the non-rick female is passing through a comparatively non-breeding phase. These observations support the idea of the rick populations forming a reservoir which may augment the rural rat populations during the following summer unless

steps are taken to eliminate them at threshing time. It seems important that ricks should be threshed as early as possible, both from the point of view of damage to the ricks while they are serving as cover for these rat populations, and of preventing their relatively high potential rate of increase in numbers.

### 8. Density of mouse populations

In Table 3 the approximate density of active (i.e. non-nestling) mice per rick is expressed in terms of six arbitrary groupings. It will be seen from this table that during 1939–40 the mouse populations tended to increase as the season advanced, while during 1940–1 the trend, if any, is not very apparent from the distributions. In order to express in a single figure the approximate density of active mice per rick in the various 4-week periods, the average class size was taken for all rick groups reporting the presence of mice. The results were as follows:

| | Average class size of active mouse populations | |
|---|---|---|
| | 1939–40 | 1940–1 |
| 17 Sept.–14 Oct. | — | 2·71 |
| 15 Oct. –11 Nov. | — | 2·54 |
| 12 Nov.– 9 Dec. | 1·33 | 1·73 |
| 10 Dec. – 7 Jan. | 1·25 | 2·31 |
| 8 Jan. – 4 Feb. | 1·50 | 2·83 |
| 5 Feb. – 4 Mar. | 2·38 | 2·72 |
| 5 Mar. – 1 Apr. | 2·33 | 2·35 |
| 2 Apr. –29 Apr. | 2·43 | 2·80 |
| 30 Apr. –27 May | 3·17 | 3·00 |
| 28 May –22 July | 3·20 | 2·33 |

In the first season the average class size tended to increase as the season advanced. In the second season the figures were very irregular, and during the winter months—say from 12 November to 4 March—they appeared to be higher than in 1939–40. It seems likely that this apparent difference was due, in part at least, to the fact that between 12 November and 4 March several rick groups were threshed which, owing to their proximity to mills, were especially liable to an early and heavy mouse infestation.

It must be emphasized that these figures for the mouse populations are extremely rough. Their importance, however, appears to us to be in emphasizing that there is a 'mouse problem' which is as equally important as the 'rat problem' in corn ricks. It is difficult to assess the damage which a mouse population does to a rick: possibly it is not on the same dramatic scale as that which may be done by rats, but nevertheless from the known habits of house-mice it must be considerable (including the gnawing through of the strings that bind the sheaves); and we have records of ricks, empty of rats but heavily mouse infested, with very serious grain damage. A class 3 population in the above terminology, the degree of infestation reached in both seasons round about May, corresponds very roughly to an average of 75 active mice per rick. In November in both years the average number was round

about 20 mice, so that in 6 months the mouse population may multiply—either through births or immigration or both—roughly just over $3\frac{1}{2}$ times.

### 9. Predators in ricks

Much has been recorded, largely in a rather casual form in sporting magazines, on the importance of predators in controlling the numbers of harmful small mammals. Some of the better references are given below.

Ticehurst (1935, 1939), from pellet analysis, gives the following table:

| Short-tailed field-vole | Common shrew | Long-tailed field-mouse | Pigmy shrew | Brown rat | House-mouse | Water-vole | Mole | Water shrew | Bird | Bank-vole | Expressed in % of food |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 33·2 | 31·5 | 12·1 | 3·1 | 9·7 | 5·1 | 0·13 | 1 | 0·2 | 3·5 | ? | Barn owl |
| 36 | — | 32·5 | — | 6·7 | 0·4 | 0·3 | — | — | 19·9 | 2·8 | Long-eared owl |

Hibbert-Ware (1937–8) gives the contents of eight little owl nests. Five contained the remains of six rats and six contained the remains of 26 house-mice. During the 1936 enquiry she records: 'The remains of rodents were found as follows: rabbits, 17; rats, 50; mice, 220; voles, 141; mice or voles, 42, giving a total for the year 1936 of 470 rodents. During the nesting season large and medium-sized rats and young rabbits were taken.... The rats found during the rest of the year were usually small but often larger than mice. Mice, voles and young rats were found in the pellets throughout the year. In open country they occurred occasionally; on the edge of woodland and in enclosed fields they formed an important part of the diet.'

Hosking (1941), in Norfolk during early May, watched at a long-eared owl's nest for a few nights shortly after the young had hatched. The male paid five or six visits per night to the nest with food. The female was mostly brooding but brought food (a full-grown rat) once. Hosking usually could not see the prey in the darkness, but he actually identified 19 rats (18 being 'young of various sizes'), seven field-mice and two field-voles.

Collinge (1913) says that of 108 tawny owl pellets examined, rat remains occurred in 12. Quoting Adams (1898) he says that of 1124 barn-owl pellets examined, rat remains occurred in 205 and house-mouse remains in 29.

Collinge (1924–7) gives diagrammatic representations of the food of some of the British owls:

Barn owl: 77·5 % of food shown as small mammal.

Long-eared owl: 82 % of food shown as small mammal.

Short-eared owl: 80·5 % of food shown as small mammal.

Tawny owl: 85·5 % of food shown as small mammal.

With the sparrowhawk, 6·5 % of food is shown to consist of mice (of the remainder, 66 % consists of birds). 323 kestrel pellets were examined and 11 rats and 10 house-mice were identified in them. He states that 64·5 % of the total food consists of 'Mice, voles, etc.'

Southern & Watson (1941), from stomach examination of 51 red foxes, found only 1·7 % of the food to consist of rat and 5·3 % of 'small rodents'.

Kalabukhov & Raevskii (1933, 1935) ringed several hundred house-mice (*Mus musculus*) in the winter around a village in the North Caucasus region and collected pellets of birds of prey in the vicinity. They found that these birds ate at least 1·4–1·6 % of the ringed mice daily. In the first work predator pellets were collected in various rural areas in this district at different times. The number of house-mouse remains—expressed as percentage of total small mammal remains—was as follows:

| | |
|---|---|
| December: 58 and 80 %. | February: 22, 24 and 41 %. |
| January: 37, 54 and 60 %. | March: 68 %. |

Bacteriological investigations on house-mice in corn ricks showed a complete absence of infective diseases, and the writers consider that predators are the main factor in controlling the rodent numbers. It would seem that owing to the cover afforded by ricks, the rodents there stand their maximum chance of escaping.

Our own observations of predators found in corn ricks at threshing are not very conclusive but are worth placing on record:

*Weasel* (*Mustela nivalis*). Localities 101 and 102 (Wytham, near Oxford) were threshed in late December 1939 and early January 1940. The ten ricks contained 147 active rats and one occupied nest, about 68 active mice and two occupied nests. In between threshing these two farms the tackle threshed two wheat ricks at an intermediate group of buildings. L. S. V. V. did not visit this place, but the foreman said that a weasel was living in the ricks and that they contained no rats and only a very few mice.

A group of two oat ricks (16/J and K, Compton, Berkshire) was threshed 3–4 July 1940, having been standing since mid-September 1939. Together they contained 117 active rats and 10–11 occupied nests; about 130 active mice and about six occupied nests. In one rick was a weasel nest, 5 ft. up and 1 ft. in, with four young (three female and one male averaging 51 g. each). Their stomachs contained mouse hair. One adult was seen to escape from the rick. The rick with the weasels had 67 of the active rats and one to two of the nests; 50 of the active mice and two of the nests.

A group of two oat ricks (10/DD and EE, Compton, Berkshire) was threshed on 3–4 March 1941, having been standing since about 20 August 1940. They contained 14 active rats, no mice and no nests. A female weasel, weighing 60 g., was in the rick containing six rats.

A semi-Dutch barn (428, Barford, Warwickshire) was filled with wheat in early September 1940 and was threshed 25–27 June 1941. Seven active rats and one occupied nest were found. There had obviously been many more rats (much dung came through with the grain), but they were leaving the rick by late June. Mice were stated to be 'impossible to estimate', and it was thought that several hundred were present. The nests were not counted. High in the rick was a barn owl's nest with eggs (not counted), and low down was a nest containing four young weasels. Both adult weasels were present in the rick but escaped. A number of mice escaped at threshing by hiding in the litter on the barn floor and, later, the place was reported to be still infested. Both barn owls and weasels were still seen to be hunting this litter-covered floor and the surroundings of the barn and when it was cleared up on 18 July only four mice and one dead rat were found. Fifty breakback traps, put down the same night, caught only two mice. It seems improbable that the mice

had left, because the litter was rich in grain and the barn was surrounded by a large expanse of arable land with very little suitable cover. Mice would obviously become an easier prey when they had no rick to hide in and were only living in loose litter.

Fenyuk (1937) has written a general summary of the problem of rodent infestation in stacked crops in the U.S.S.R. He notes that small rodents seek such cover. In an early summer rodent census of 16 hectares of a wheat field in Stalingrad Province, only eight house-mice (*Mus musculus*) and one vole (*Microtus arvalis*) were caught; but on going through three small straw stacks of the previous year the catch was 11 house-mice and 338 voles.

*Stoat* (*Mustela erminea*). Wheat rick 492/A (South Leigh, Oxfordshire) was threshed on 31 December 1940, having been built in mid-August of the same year. It contained one live and two half-eaten rats, no mice and no nests. An adult stoat was found to be living in the rick.

A group of two oat ricks (466/K and L, Berrick Salome, Oxfordshire) was threshed 12–14 May 1941, having been standing since the last week of August 1940. 466/K contained no rats and 150–200 mice with 10–15 occupied nests. 466/L contained no rats and about 100 mice with about eight nests. In this latter rick was an adult stoat (escaped) and a nest about 5 ft. up with five young (three males and two females averaging 50 g. each).

*Barn owl* (*Tyto alba*). Oat rick 10/U (Compton, Berkshire) had a tunnel running into the middle at eave-level for cooling purposes. The rick was built in late August 1939 and not threshed until 25 June 1940. A barn owl's nest was found at the end of the tunnel with two small and two large young. L. S. V. V. was not present at threshing, but the men on the rick said that many rat and mouse remains were lying in the tunnel. Four pellets or remains were saved and these contained:

Pellet 1: bones and fur of rat, complete except for part of skull.

Pellet 2: bones and fur of rat; skull not present.

Pellet 3: bones and fur of *Microtus agrestis* and part of skull and some bones of rat.

No. 4: back legs with bones, fur and tail of rat.

The rick had 26 active rats and two occupied nests. The mouse population was estimated at about 500 (probably an overestimation).

Dutch Barn 428 had a barn owl's nest in it when threshed 25–27 June 1941 (see above).

Our evidence is at present too scanty to permit of any generalization on the importance of the influence of predators on corn-rick rat and mouse populations. It can, of course, be truthfully stated that owls, many hawks, weasels, stoats, etc., *do* kill rats and mice, and that in a few instances, at any rate, such predators live and even breed in cornstacks containing high rodent infestations.

## 10. Other rodents in ricks

The presence of stoats and weasels in corn ricks is discussed in the previous section. Harvest mice (*Micromys minutus*), long-tailed field-mice (*Apodemus sylvaticus*) and a bank-vole (*Clethrionomys glareolus*) have also been recorded from some of our ricks, but it must be understood that these have only been found when L. S. V. V. was present at threshing. Such small animals would be classed as 'mice' by the workmen, if indeed they were noticed at all.

Bean rick 412/A in the rickyard of Manor Farm, Lyford, Berkshire, was built in the first week of September 1939. When threshed on 21–22 February 1940 it contained six rats and two occupied nests, and 26 house-mice and two occupied nests, and seven adult long-tailed field mice (four non-pregnant females and three males).

Wheat rick 111/M in a field near Red Barn Farm, Wolvercote, Oxford, was built in mid-August 1940. When threshed on 25 October it contained two rats and one occupied nest, four house-mice and one occupied nest and one adult male long-tailed field-mouse (non-breeding).

Oat rick 497/A in a field at Church Farm, Little Wittenham, Berkshire, was built on 20 August 1940. When threshed on 15 January 1941 it contained 20 rats and no occupied nests, about 100 mice and about 12 occupied nests and one adult bank-vole.

Wheat rick 453/J in a field at Radcot Farm, Appleford, Berkshire, was built in mid-August 1940. When threshed on 5 May 1941 it contained five rats (but rats had no doubt started to leave the rick by then) and no occupied nests, 25–30 house-mice and one occupied nest; and also two adult harvest-mice.

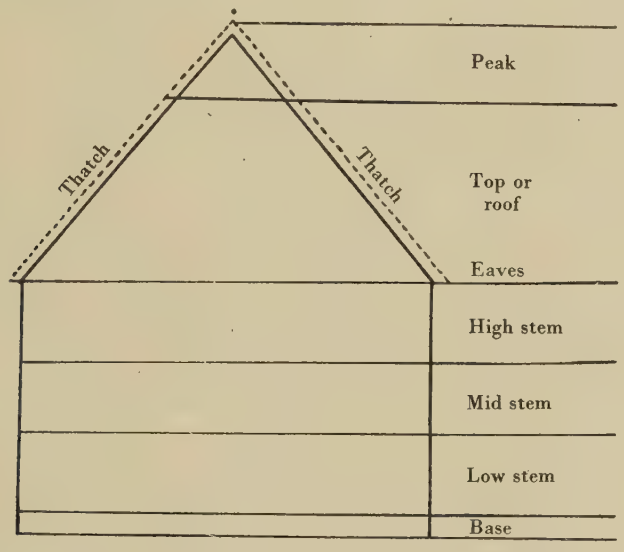


Fig. 3. Diagram of corn rick. Explanation of terms. Side elevation of round rick or end elevation of rectangle rick.

## 11. RAT-MOUSE RELATIONSHIP IN RICKS

A high rat population in a rick does not necessarily exclude a high mouse population. This was noted in the field work when we sometimes killed 50 or more active rats and about 100 active house-mice from the same rick—both species breeding. When a rick is being threshed, the rodent population is greatly disturbed and tends to work down to the base as the men get lower and lower. Therefore the height at which rats and mice bolt is not of any great significance—a few may bolt from anywhere but most bolt from the base. The general impression gained from being present at the threshing of many ricks and watching for nests and dung distribution, is that the majority of the rats live high in the rick and the majority of the mice live low down. There must, however, be a considerable overlap, especially as a few rats will quite often be found breeding in the base. When the thatch is being pulled off, preparatory to threshing, one generally does not see any mice, but not

infrequently a few rats are bolted. However, one rick reported by a foreman as containing 'hundreds' of mice and no rats had mouse nests and damage extending right through the rick.

L. S. V. V. was present right through the threshing of a group of six badly infested wheat ricks in March 1940 (Locality 111), and particular attention was paid to the distribution of nests (both new and old). This distribution confirmed the impression stated above. In tabulating the distribution of the old nests (notes were kept in four ricks only) the following categories are used for the sake of brevity (see Fig. 3): 'Few', 'Thinly distributed throughout section', 'Common'. Table 6 shows the number of times the various categories were found at the different levels. With the occupied nests complete counts are used.

Table 6. *Old nests*

*Out of four ricks the number of times the categories were found at different levels*

| | Brown rat | | | House-mouse | | |
|---|---|---|---|---|---|---|
| | Few | Thinly distributed | Common | Few | Thinly distributed | Common |
| Peak | 1 | 1 | 2 | — | — | — |
| Top | 1 | 1 | 2 | 2 | — | — |
| High stem | — | 4 | — | 2 | — | — |
| Mid stem | 1 | 3 | — | 4 | — | — |
| Low stem | 2 | 1 | — | — | 4 | — |
| Base | 2 | — | — | — | 1 | 3 |

*Number of occupied nests observed in all six ricks*

| | Brown rat | House-mouse |
|---|---|---|
| Peak | 2 | — |
| Top | 5 | — |
| High stem | 7 | 1 |
| Mid stem | 6 | 4 |
| Low stem | 1-2 | 6 |
| Base | 6 | 10 |

## 12. Summary and discussion

(1) *Survey.* A series of records was obtained of the numbers of rats (*Rattus norvegicus*) and house-mice (*Mus musculus*) found at threshing time in 518 individual corn ricks forming a total of 266 rick groups in Oxfordshire and Berkshire. In the first season (1939–40) only those ricks having a moderate or heavy degree of rat infestation were recorded (45 rick groups formed by 99 ricks). During the second season (1940–1) a more complete survey was undertaken of all ricks which were threshed by three contractors' tackles and by the Agricultural Research Council's field station at Compton (266 rick groups or 419 ricks).

(2) *Records.* A return was made for each rick of the number of rats killed or seen escaping, together with the number of occupied nests. A large number of these rats were sent in and examined in the laboratory, thus providing a

valuable series of data on the age composition, sex ratios and pregnancy rates observed in these rick populations. It is hoped, in due course, to publish fully the results obtained from this section of the work; the present paper is devoted to the results of the field work, more particularly in regard to the rat populations found inhabiting the corn ricks. Although similar returns were made for the number of mice and of mouse nests, these data can, at present, only serve as rough indications of the degrees of mouse infestation observed.

(3) *Census of rats.* When the work was started in November 1939, the mean number of active rats per rick was around 16 and the mean total population of all ages nearly 18. These figures rose until April 1940, when the peak period of density was reached with a mean number of 57 active rats and 79 total population. After April 1940 the density per rick fell and there appeared to be evidence that a number of rats in the ricks still standing had been emigrating into the fields and hedges. The last ricks threshed in June and July 1940 were found to contain an average of 28 active rats and a mean total population of 42.

During the second season the figures for rats were much lower: but a direct comparison with the preceding season cannot be made, since a much wider sample of all degrees of infestation was collected during 1940–1. The figures for the second season were an average of two to three active rats per rick or a total population of four during September–November 1940, rising, though much more irregularly than in the first season, to a peak of 33 active rats and a total population of 45 during April 1941. In May and June 1941 an average total population of 36 rats per rick was recorded.

(4) *Grain preference of rats.* There is a popular belief in country districts that oat ricks tend to be less infested with rats than wheat ricks, and it would have been interesting to see if these collected figures afforded any numerical evidence whether this belief was sound, or, in general, whether any particular type of grain was preferred to another. The measurement of any such preference, however, presents many and grave difficulties, and these data are not extensive enough to warrant any detailed discussion of this point. But so far as the present evidence goes, it would seem fairly safe to say that where rats are present on a farm, no type of grain rick is exempt from the possibility of being colonized, and that in all types a relatively large rat population may be found, depending on the time of year at which the rick group is threshed.

(5) *Breeding rates of rats.* A marked and significant difference was observed during the winter months between the percentage of adult females pregnant in the rick populations and the same percentage in females coming from other environments and habitats, e.g. hedges, banks, county refuse dumps, etc. Thus between November 1939 and February 1940 some 28 % of adult rick females were found to be pregnant compared with only 3 % of

non-rick females. Similar differences were also apparent during the second season.

(6) *House-mouse census.* The information obtained about the mouse populations was less accurate and less complete than that for rats. Nevertheless, it was sufficient to show that there is a mouse problem every bit as serious as the rat problem in regard to corn ricks. Their numbers and the amount of damage they do to the stacked corn is very difficult to assess. But certainly very large mouse populations may be found even quite early in the season, and it is the firm conviction of many countrymen that they may do even more damage than the rats. Both rats and mice can coexist in relatively large numbers, and we have a certain amount of evidence to show that under these conditions there is a regional distribution of the respective nests, rats tending to concentrate in the upper half of the rick and, frequently, in the extreme base while mice are tend to be found in the lower half of the stem of the rick.

(7) *Validity of records.* In regard to the numerical part of this investigation a word of caution is necessary. It is always a matter of some difficulty to collect accurate figures under conditions where the principal object is not in the first place to amass scientific data, but to complete the practical job of threshing a corn rick in as short a time as possible. Moreover, in order to sample a sufficiently representative area during the second season, it was necessary to rely almost entirely on the reports sent in by the three threshing-tackle foremen, since it was a physical impossibility for one of us to be present at all the ricks threshed. The first season's work, however, gave L. S. V. V. the opportunity of working in conjunction with these foremen and of explaining the object of the survey and the type of data it was necessary to collect.

In so far as the number of active rats is concerned, we believe that the figures are reasonably accurate. As we have already pointed out, these rats arouse the sporting instincts of the men and dogs and, with the help of the wire netting which was placed round nearly every rick, were for the most part killed and could therefore be easily counted at the end of the day. A fair idea could also be formed of the number which had managed to escape. Our impression is that the greatest source of error in these figures, when it was present, was in regard to the number of rat nests. In the rush of work involved in dismantling a rick, it is possible that a certain number of nests containing newly born young *may* have been overlooked. This, however, is an impression and nothing more; we have no actual evidence as to what extent it may have been present as a source of error. Compared with the rat figures, those for the mice are much less accurate and we have already discussed in § 5 the difficulties involved in assessing the degree of mouse infestation. The methods used in the text must be taken as being highly approximate.

(8) *Corn-rick rat control.* Apart from these provisos, it seems clear that these observations, both in regard to the number of rats and the amount of breeding, support the view of the corn rick as a habitat of major importance in the ecology of country rat populations. It is desirable that similar investigations should be carried out in other parts of the country. The results so far obtained stress the importance of early threshing, in order to prevent the relatively large increase in numbers and resulting damage which may take place in some years, and also of killing all rats found when the rick is dismantled, which is now compulsory by law. It may be remarked that a government policy of controlled corn prices tends strongly to encourage early threshing, while one of subsidizing storage in the rick, acts, of course, in the opposite way.

(9) *Gassing rats in ricks.* A proprietary brand of cyanide gas powder was pumped into two wheat ricks by the head field demonstrator of the firm in co-operation with L. S. V. V. Five pounds per rick were used and the instructions on the tin were followed—gassing and plugging the lowest holes first and working upwards to the peak. On threshing these ricks on the following day it was found that only a third of the rats were dead—12 out of 35 and 3 out of 10 (there were only two mice in the ricks and both were dead).

(10) *Protection of corn ricks.* Protection of corn ricks against rodent infestation appears to be quite uneconomical. A 3 ft. fence (to surpass the rats' jumping powers) buried 1 ft. to prevent them digging underneath it, made of some such material as sheet iron, would be necessary. Wire netting does not afford protection: mice can squeeze through almost any hole and an adult male brown rat ('wild' but in captivity, at the Bureau) climbed a fence of three-eighths mesh wire netting 3 ft. high with a horizontal overhang of 1 ft. at the top, at the end of which was a hanging fringe 7 in. deep.

Staddles are now practically non-existent on farms and are unpopular owing to the increased height of the rick and because constant supervision is necessary, until the rick is threshed, to see that hanging straws, wind-blown debris or carelessly placed tools do not afford a possible climbing or jumping place for rats and mice. They are usually too low.

At present early threshing would certainly seem to be the best all-round policy for corn ricks.

(11) *Other species in corn ricks.* Some observations were made on other animals found living in the corn ricks so far worked. These are the bank-vole (*Clethrionomys glareolus*), long-tailed field-mouse (*Apodemus sylvaticus*), harvest-mouse (*Micromys minutus*) and, of the predators, stoat (*Mustela erminea*), weasel (*Mustela nivalis*) and barn owl (*Tyto alba*). In many cases when a predator was found living in a rick, there was a high rodent population as well. It seems probable that the predators were attracted by this aggregation of potential food but, owing to the cover afforded by the rick, much of the prey escaped capture.

We would like to express our appreciation of the co-operation received from Dr G. Dunkin and Mr E. A. MacMillan of the Agricultural Research Council Estate at Compton; and also from the three threshing-tackle foremen: Mr G. Baggott of Curtis's, Oxford; Mr A. Thatcher of Thatcher's, Abingdon and Mr T. Yeo of Wilder's, Wallingford. We would also like to thank Mr Charles Elton and other colleagues of the Bureau of Animal Population for their assistance in handing over to us data from certain localities, and especially Miss U. M. Wykes who has been chiefly responsible for the laboratory examination of the rats.

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## APPENDIX

(Names follow the check-list of British Vertebrates (1935), British Museum (Natural History).)

| | | | |
|---|---|---|---|
| Mole | *Talpa europaea* | Long-tailed field-mouse | *Apodemus sylvaticus* |
| Common shrew | *Sorex araneus* | Harvest-mouse | *Micromys minutus* |
| Pigmy shrew | *Sorex minutus* | Brown rat | *Rattus norvegicus* |
| Water shrew | *Neomys fodiens* | House-mouse | *Mus musculus* |
| Fox | *Vulpes vulpes* | | |
| Stoat | *Mustela erminea* | Barn-owl | *Tyto alba* |
| Weasel | *Mustela nivalis* | Long-eared owl | *Asio otus* |
| Rabbit | *Oryctolagus cuniculus* | Short-eared owl | *Asio flammeus* |
| Bank-vole | *Clethrionomys (Evotomys) glareolus* | Tawny owl | *Strix aluco* |
| | | Little owl | *Carine noctua* |
| Water-vole | *Arvicola amphibius* | Sparrowhawk | *Accipiter nisus* |
| Short-tailed field-vole | *Microtus hirtus* | Kestrel | *Falco tinnunculus* |

# STUDIES OF FLUCTUATIONS IN INSECT POPULATIONS

## IX. THE CARROT-FLY (*PSILA ROSAE*) IN 1936–41

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(*With Plate 2 and 3 Figures in the Text*)

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### 1. Introduction

In the sixth of these studies (**1**) it was stated that only two of those on gall midges were to be continued, namely, that on the wheat-blossom midges and that on the button-top midge of willows. The latter has since been brought to a conclusion (**2**), except for the temporary omission of a discussion of the emergence of the midge's parasites and the relative numbers of the various species involved. The study of the wheat-blossom midges has been brought up-to-date by an account of the midges during the years 1932–40 and a discussion of the results obtained 1927–40 (**3**). It is intended that this particular study shall be continued.

It was stated (**1**) that preparations were being made to begin similar studies on other insects, such as the cabbage white fly and some cutworms or surface caterpillars. It was found impracticable to carry out these studies. But in 1936 investigations were begun on the common leatherjacket or crane-fly (*Tipula paludosa* Meigen) and the carrot-fly (*Psila rosae* F.). Two preliminary reports have already been published (**4**, **5**) on *Tipula paludosa*, actual population figures for the years 1937–40 being presented in the second of these two papers. In the present paper it is proposed to give the results of the carrot-fly investigation.

I am greatly indebted to Mr A. Roebuck of the Midland Agricultural College, both for his actual assistance in collecting the material which made this study possible, and for his help in planning and discussing various aspects of the problem.

## 2. Methods

It was hoped by this study to obtain figures for the comparative abundance of the carrot-fly from year to year and the variations in parasitism and in emergence dates. It was decided that it would be preferable to obtain material from two areas in which carrots only were chiefly grown rather than from those in which carrots, celery and parsnips, the fly's main alternate host plants, were grown in considerable quantities. For this reason, the area round Scotter in north Lincolnshire and that round Collingham in east Nottinghamshire were selected as the two localities from which to draw material. Sampling was done in the two areas on successive days except in 1941.

The actual farms and fields to be sampled each year were decided upon by information as to the heaviest infestation, supplied by the growers and men in charge of carrot-washing sheds. The material was collected each year in February and early March, either from opened pie or clamp bottoms for choice, or from carrots still in the rows, and on one occasion from empty rows from which the carrots had been recently lifted to be washed.

In order to attempt to assess the varying abundance of the carrot-fly, the time taken to collect the material was noted. In the north Lincolnshire area collecting lasted 3, $4\frac{1}{2}$, 3, 1, and $1\frac{1}{2}$ hr. respectively in the years 1936–40, and for the east Nottinghamshire area the corresponding figures are $1\frac{1}{2}$, 3, 3, 3, and 2 hr. The materials collected by Mr Roebuck and the author were kept separate so as to enable the personal collecting rate to be assessed.

The larvae and puparia were transferred in soil taken from the locality in which they were found. After resorting and counting they were placed in the original soil in pots which were kept in darkened chambers with glass emergence tubes in the unheated insectary at Rothamsted Experimental Station.

With the exception of two individuals, one in each of the years 1937 and 1938, the only parasite obtained was *Dacnusa postica* Hal., for whose identification I am indebted to the Imperial Institute of Entomology. It was noticed that some larvae, and in one year some puparia, were dying from some blackening disease. Exact figures for the prevalence of this disease were not kept, but it appears more common in excessively damp seasons. Larvae and puparia so affected were rejected, but the low percentage emergence figures in some years may possibly be accounted for by part of the material having this disease in an incipient and unnoticeable stage.

## 3. Data obtained

The amount of material studied and the number of flies and parasites reared each year are given in Table 1.

What may be termed the sampling results are given in Tables 2 and 3. These show the dates of sampling and the position from which the larvae and puparia were collected. In addition, the number of larvae and puparia are given as well as the rate of collecting per hour.

1

2 3

Fig. 1. Carrot-fly × 5.

Fig. 2. Larva × 6.

Fig. 3. Attacked carrot nat. size.

(Reproduced from *Adv. Leafl. Minist. Agric. Fish. Lond.*, 68 (edition 1941), by kind permission of the Controller of H.M. Stationery Office.)

Table 1. *Material studied, (A) larvae and puparia put to breed and (B) carrot-flies and parasites reared*

| Year | North Lincolnshire, near Scotter (A) | North Lincolnshire, near Scotter (B) flies–parasites | East Nottinghamshire, near Collingham (A) | East Nottinghamshire, near Collingham (B) flies–parasites |
|---|---|---|---|---|
| 1936 | 136 | 102– 4 | 33 | 6– 0 |
| 1937 | 351 | 296–16* | 276 | 218– 5 |
| 1938 | 725 | 599–46* | 294 | 243–10 |
| 1939 | 455 | 358–26 | 795 | 613– 4 |
| 1940 | 295 | 95–33 | 411 | 252–58 |
| 1941 | 645 | 476–53 | 650 | 465–48 |

* In addition one small parasite emerged from the material in each of these two years.

Table 2. *Dates and position of sampling, numbers of larvae and puparia found and rate of collecting per hour in north Lincolnshire*

| Year | Date | Position | Larvae | Puparia | Ratio larvae : puparia | Rate of collecting per hr. |
|---|---|---|---|---|---|---|
| 1936 | 19 Feb. | Opened pies | (*a*) 24 | 4 | 86 : 14 | 9 |
| | | | (*b*) 123 | 10 | 92 : 8 | 44 |
| 1937 | 19 Feb. | Carrots in rows | (*a*) 78 | 62 | 56 : 44 | 31 |
| | | | (*b*) 111 | 100 | 53 : 47 | 47 |
| 1938 | 3 Mar. | Empty rows | (*a*) 80 | 263 | 23 : 77 | 114 |
| | | | (*b*) 79 | 246 | 24 : 76 | 108 |
| | | | (*c*) 20 | 39 | 34 : 66 | — |
| 1939 | 28 Feb. | Sifted soil from clamp | (*a*) 38 | 83 | 31 : 69 | 121 |
| | | | (*b*) 12 | 164 | 7 : 93 | 176 |
| | | | (*c*) 58 | 100 | 37 : 63 | — |
| 1940 | 27 Feb. | Carrots in rows, opened pies | (*a*) 115 | 18 | 86 : 14 | 89 |
| | | | (*b*) 110 | 76 | 57 : 43 | 117 |
| 1941 | 25 Mar. | Opened pies | (*d*) 14 | 861 | 0·5 : 99·5 | — |

*Notes.* Material collected by (*a*) A. Roebuck, (*b*) H. F. Barnes, (*c*) A. Roebuck and H. F. Barnes jointly, (*d*) A. Roebuck and helpers.

Table 3. *Dates and position of sampling, numbers of larvae and puparia found and rate of collecting per hour in east Nottinghamshire*

| Year | Date | Position | Larvae | Puparia | Ratio larvae : puparia | Rate of collecting per hr. |
|---|---|---|---|---|---|---|
| 1936 | 20 Feb. | Opened pies | (*c*) 32 | 1 | 97 : 3 | 22 |
| 1937 | 18 Feb. | Carrots in rows | (*a*) 52 | 43 | 55 : 45 | 32 |
| | | | (*b*) 99 | 82 | 54 : 46 | 60 |
| 1938 | 2 Mar. | Opened pies | (*a*) 53 | 41 | 56 : 44 | 31 |
| | | | (*b*) 138 | 59 | 70 : 30 | 66 |
| 1939 | 27 Feb. | Opened pies | (*a*) 12 | 278 | 4 : 96 | 97 |
| | | | (*b*) 13 | 492 | 3 : 97 | 168 |
| 1940 | 26 Feb. | Opened pies | (*a*) 87 | 12 | 88 : 12 | 50 |
| | | | (*b*) 263 | 60 | 81 : 19 | 162 |
| 1941 | 3 Mar. | Opened pies | (*d*) 61 | 831 | 7 : 93* | — |

*Notes.* (*a*), (*b*), (*c*) and (*d*) as in Table 2.

* The material was re-sorted on 31 Mar.; at the time of sampling, the larvae : puparia ratio was 89·5 : 10·5.

The results of breeding the material so collected are given in Tables 4 and 5. The numbers of carrot-flies and parasites which emerged are shown as well as the sex ratio of the carrot-flies, the relative parasitism and the percentage emergence of the material under investigation.

Table 4. *Numbers of carrot-flies and parasites which emerged, percentage emergence, sex ratio of carrot-flies and relative parasitism. North Lincolnshire material*

| Year | Material | Carrot-flies–parasites ♂ – ♀ – *p* | % emergence | Carrot-fly sex ratio | % relative parasitism |
|---|---|---|---|---|---|
| 1936 | (*a*) and (*b*) | 42– 57– 4 | 81 | 42 : 57 | 3·9 |
| 1937 | (*a*) | 57– 67– 7 | 94 | 46 : 54 | 4·6 |
| | (*b*) | 84– 88–10 | 88 | 49 : 51 | 5·5 |
| 1938 | (*a*) | 121–157–25 | 88 | 44 : 56 | 7·9 |
| | (*b*) and (*c*) | 165–154–22 | 89 | 52 : 48 | 6·5 |
| 1939 | (*a*) | 47– 47– 4 | 82 | 50 : 50 | 4·0 |
| | (*b*) | 64– 76– 8 | 85 | 46 : 54 | 5·3 |
| | (*c*) | 47– 74–14 | 85 | 39 : 61 | 10·4 |
| 1940 | (*a*) | 20– 28–14 | 48 | 42 : 58 | 23·0 |
| | (*b*) | 20– 26–19 | 40 | 43 : 57 | 29·0 |
| 1941 | (*d*) | 187–278–53 | 82 | 40 : 60 | 10·0 |

*Notes.* In addition to the number of male and female carrot-flies listed as having emerged, some few flies were seen to escape from the emergence tubes. For explanation of (*a*), (*b*), (*c*) and (*d*) see Table 2.

Table 5. *Numbers of carrot-flies and parasites which emerged, percentage emergence, sex ratio of carrot-flies and relative parasitism. East Nottinghamshire material*

| Year | Material | Carrot-flies–parasites ♂ – ♀ – *p* | % emergence | Carrot-fly sex ratio | % relative parasitism |
|---|---|---|---|---|---|
| 1936 | [(*a*) and (*b*) | 3– 3– 0 | 18 | — | Nil] |
| 1937 | (*a*) | 31– 47– 1 | 83 | 40 : 60 | 1·3 |
| | (*b*) | 51– 89– 4 | 80 | 36 : 64 | 2·8 |
| 1938 | (*a*) | 35– 46– 3 | 90 | 43 : 57 | 3·5 |
| | (*b*) | 69– 92– 7 | 84 | 43 : 57 | 4·2 |
| 1939 | (*a*) | 124–129– 2 | 88 | 49 : 51 | 0·8 |
| | (*b*) | 149–210– 2 | 72 | 42 : 58 | 0·55 |
| 1940 | (*a*) | 18– 28–15 | 63 | 39 : 61 | 24·0 |
| | (*b*) | 95–110–43 | 79 | 46 : 54 | 17·0 |
| 1941 | (*d*) | 178–278–48 | 79 | 39 : 61 | 9·4 |

*Notes.* See Table 4.

## 4. Discussion of results

### (*a*) *The choice of site for sampling*

In order to select the best site for sampling, reliance was placed upon growers and those at washing sheds indicating the farms and fields suffering the most severe damage. This was inevitable owing to the distances that had to be travelled, the time available and the lack of financial assistance which would have resulted in adequate teams of investigators. Nevertheless, it is

considered that the opinions of those consulted bore a close resemblance to the true state of affairs in their neighbourhood and so were a satisfactory method.

*(b) Abundance of carrot-fly from year to year*

In order to assess the varying abundance from year to year, it was decided to try out a method of collecting which involved the rate of collecting per hour.

It was planned to search for larvae and puparia in the early spring, if possible in the soil at the base of the pies or clamps, either after the carrots had been removed to the washing sheds or, if need be, while the carrots were

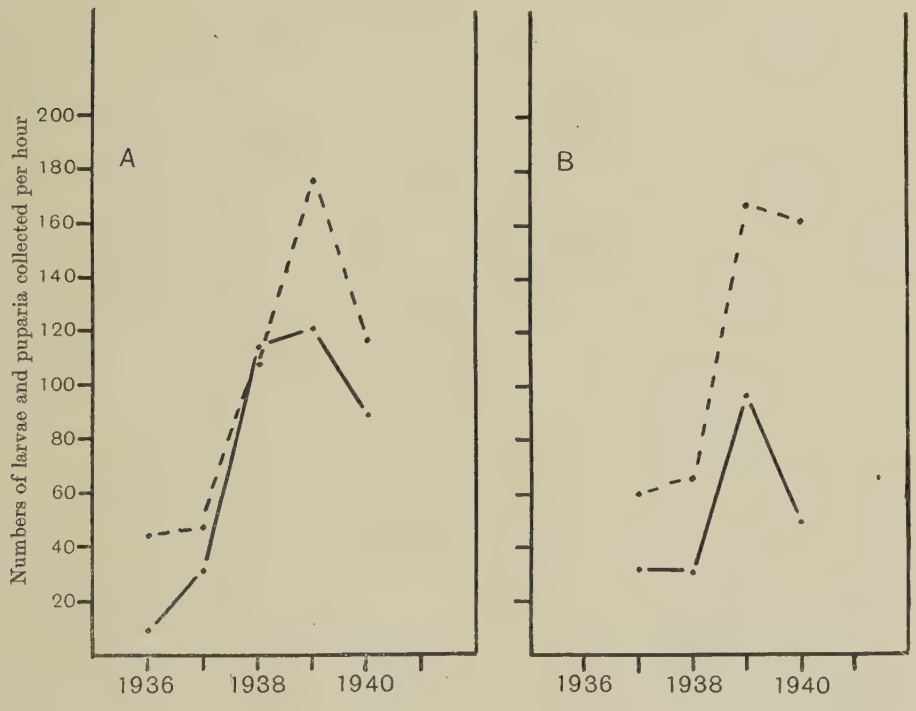


Fig. 1. Numbers of larvae and puparia collected per hour. —— by A. Roebuck, ----- by the writer. A, north Lincolnshire; B, east Nottinghamshire.

still present. It appeared reasonable to suppose that the clamps represented a concentration of the second generation and that the fully grown larvae and puparia would collect in the normal course of events in the soil immediately below the clamp. In some cases, however, the carrots had not been clamped and so it was necessary to search along the rows of carrots, either when the carrots were still present or after they had been removed direct to the washing sheds. It might have been supposed that the rate of collecting in the rows would be distinctly lower than that in clamp bottoms, but such a reduction was not noticeable. The search for larvae and puparia was continued as long

as was practicable, each collector's material being kept separate, and the duration was recorded (p. 70).

Two weaknesses inherent in this method revealed themselves. First, such a method should only be undertaken by investigators who are able to remain several days at least on the scene of operations; too much time was taken to reach the sites, thus reducing the time available for sampling. Secondly, the personal factor was very apparent in the rates of collecting per hour. Mr Roebuck usually collected at a slower rate than the writer, but it is only fair to say that Mr Roebuck always drove the car and this involved several hours' driving. The rates of collecting are given in Tables 2 and 3.

Nevertheless, the large variations found in the rates of collecting in different years as well as the similarity between the two collector's rates (Fig. 1) indicate that a comparative figure of abundance from season to season was satisfactorily obtained.

Another weakness is that two individuals are unlikely to be able to carry out such comparative sampling for more than a few years in succession. The writer was unable to sample in 1941 and the comparison thus broke down after five years.

(*c*) *Relative numbers of larvae and puparia*

The ratio of the number of larvae to puparia found (Tables 2 and 3) varied from 92 : 8 to 3 : 97. It soon became apparent that the normal sampling period (18 Feb.–3 March) was the period when the larvae were changing into puparia. The data indicate, as would be expected, that broadly speaking the earlier the date of sampling the higher the number of larvae one finds. But this is masked to some extent by the variation in 'earliness' or 'lateness' of the season, for which there is no really satisfactory measure.

The records also indicate that there is not a close direct relationship between the date of the larvae becoming puparia and that of the adult flies' subsequent emergence. It is not thought reasonable to attribute this finding to the fact that the material was brought from Lincolnshire and Nottinghamshire to Hertfordshire for rearing. Finally, there is a suggestion that the rate of collecting increases when more puparia are present than larvae.

(*d*) *Percentage emergence*

The percentage emergence (Tables 4 and 5) of flies and parasites from the larvae and puparia collected has in the case of the north Lincolnshire material always been between 81 and 94 with the exception of the year 1940, when it fell to 40 and 48 in the two collectors' material. In the east Nottinghamshire material, excluding 1936 when the amount of material was insignificant, the percentage emergence has ranged between 63 and 90. It is suggested that the lower figures are partly accounted for by the presence of the blackening disease in an incipient and unnoticeable stage when the material was set up for breeding.

### (*e*) *Sex ratio of carrot-fly at emergence*

The sex ratio (Tables 4 and 5) has varied between 39 : 61 and 52 : 48 (males : females) in the case of the north Lincolnshire material and 36 : 64 and 49 : 51 in the east Nottinghamshire material. This may indicate that the males are more susceptible to lethal factors than the females, if one is justified in postulating equality of the sexes when the eggs are laid.

### (*f*) *Dates of emergence*

The dates of the carrot-fly's emergence are shown in Fig. 2. The full line represents the north Lincolnshire material, while the dotted line indicates the east Nottinghamshire material; both were kept in the unheated out-door insectary at Harpenden, Hertfordshire. It will be noticed that the emergence curve is noteworthy because of the abruptness with which the peak of emergence is usually reached and the quickness with which the majority of the flies are on the wing. There are indications also of a minor secondary peak in some years. The peaks of emergence of the north Lincolnshire and east Nottinghamshire material coincided, except in 1939 and 1941, when that of the material from Nottinghamshire was later than that of the material from Lincolnshire.

The weekly peak seems to occur round about 14 May. In 1936 and 1937 the peaks were just a little late, while in 1938, 1939 and 1940 they were slightly early, with the exception that in 1939 the peak of emergence of the east Nottinghamshire material was decidedly later. But in 1939 the shape of the emergence curve was rather different to that in each of the other years. In 1941 the emergence was appreciably later than normal.

### (*g*) *Relative parasitism at emergence*

The figures obtained for the relative parasitism are shown in Tables 4 and 5. Table 6 shows the relative parasitism obtained compared with that if all the material that did not emerge had been flies, i.e. if the method of rearing only prevented carrot-flies and not their parasites from emerging successfully. It is obvious that such an event would not alter the relationship found between one year's parasitism and the next. The parasitism found in the two collectors' material agree more closely than might have been expected. The parasitism obtained from the two collectors' mixed material (1939 (*c*)) appears to be unduly high, but it should be mentioned that this material was collected in small amounts from different fields and different positions, in fact it was rather hotch-potch.

The parasitism from year to year is shown in Fig. 3. It can be seen that with the exception of 1940 the parasitism was distinctly low.

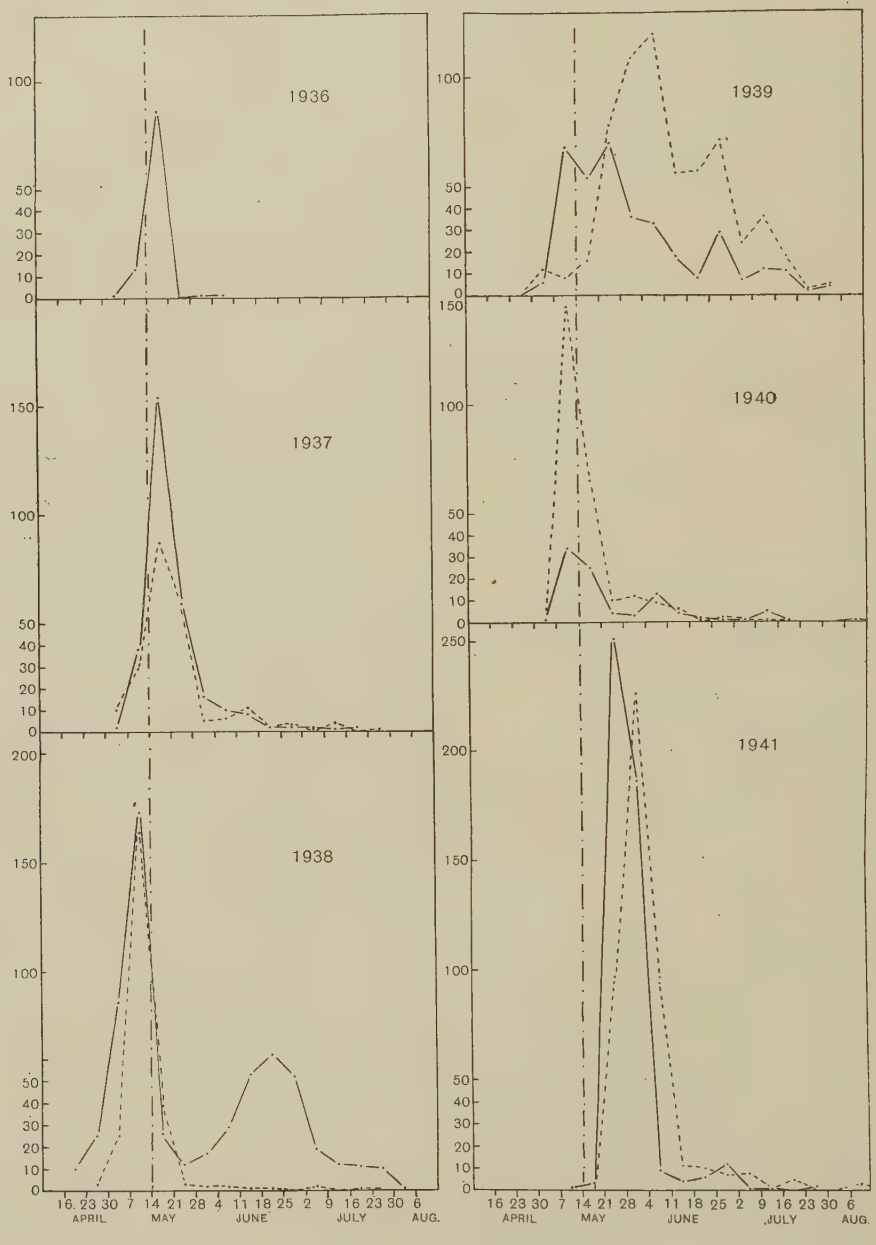


Fig. 2. Weekly emergence of carrot-flies at Rothamsted Experimental Station, Harpenden, 1936–41. —— north Lincolnshire material, ----- east Nottinghamshire material. Ordinate: numbers of carrot-flies.

Table 6. *Relative parasitism (A) obtained, (B) supposing 100% of the available parasites emerged*

| Year | | North Lincolnshire material (A) | North Lincolnshire material (B) | | East Nottinghamshire material (A) | East Nottinghamshire material (B) |
|---|---|---|---|---|---|---|
| 1936 | (*a*) and (*b*) | 3·9 | 2·9 | (*a*) and (*b*) | — | — |
| 1937 | (*a*) | 4·6 | 4·3 | (*a*) | 1·3 | 0·01 |
| | (*b*) | 5·5 | 4·7 | (*b*) | 2·8 | 2·2 |
| 1938 | (*a*) | 7·9 | 7·0 | (*a*) | 3·5 | 3·2 |
| | (*b*) and (*c*) | 6·5 | 5·8 | (*b*) | 4·2 | 3·5 |
| 1939 | (*a*) | 4·0 | 3·3 | (*a*) | 0·8 | 0·7 |
| | (*b*) | 5·3 | 4·5 | (*b*) | 0·55 | 0·4 |
| | (*c*) | 10·4 | 8·9 | | | |
| 1940 | (*a*) | 23·0 | 11·0 | (*a*) | 24·0 | 15·0 |
| | (*b*) | 29·0 | 12·0 | (*b*) | 17·0 | 11·0 |
| 1941 | (*d*) | 10·0 | 8·2 | (*d*) | 9·4 | 7·4 |

For explanation of (*a*), (*b*), (*c*) and (*d*) see Table 2.

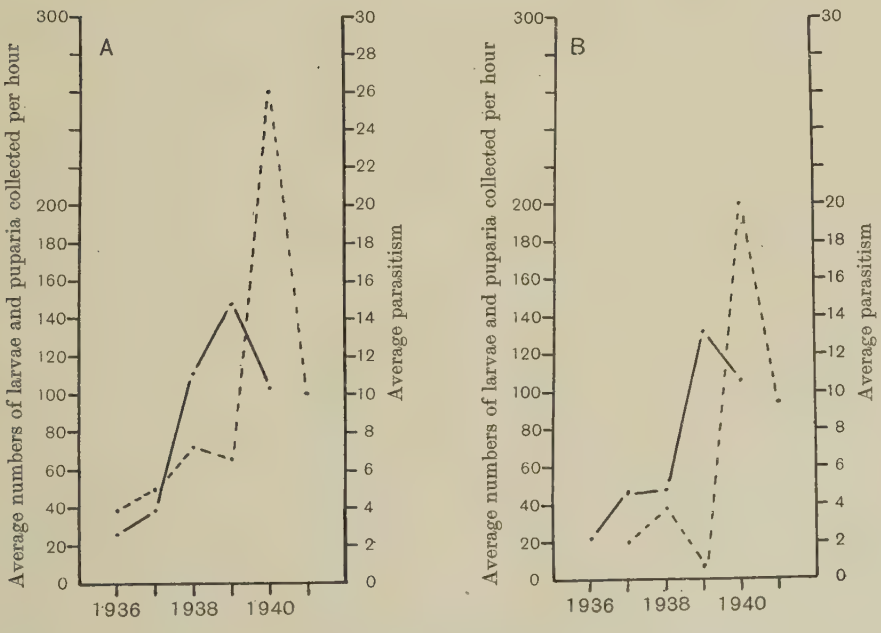


Fig. 3. Average numbers of larvae and puparia collected per hour (——) and average parasitism (-----), 1936–41. A, north Lincolnshire (Scotter) area; B, east Nottinghamshire (Collingham) area.

### 5. Recommendations for future work

It is considered that the present results have shown that the technique employed to obtain figures for the comparative abundance of the carrot-fly from year to year, the variations in parasitism and the emergence dates is justified. Not only from the point of view of obtaining records of variations in insect populations in the field but also from the point of control, it is thought that the study should be continued.

The sampling technique has its faults as already pointed out in § 4 (*b*). However, it is suggested that, in order to overcome the difficulty of being situated away from the carrot-growing area, those who do the sampling should live temporarily much closer the scene of operations. In order to minimize the personal factor in the rate of collecting, several persons should sample instead of two. This would lessen the chances of the forced absence of any sampler in any one year upsetting the whole sequence of results. Two teams of three would be a suitable number.

In view of the importance of the dates of appearance of the carrot-flies from the control point of view, it is suggested that material from different carrot-growing areas could be sent to one locality and there reared. The time of emergence in this latter locality would probably bear a constant relationship to those in the various carrot-growing areas. So long as the locality in which the material was reared was not later (? farther north) than the growing areas, it should be possible to warn such areas by telegram that carrot-fly had started emerging. This information, together with local knowledge of how much later the particular locality was, should enable advice to be given as to the dates on which active control measures against the newly emerged adults should be taken before they started ovipositing. In other words, 'Standard emergence tables' could be obtained quite easily. Tables 7 and 8 illustrate the idea.

This procedure could be applied to other insects without involving much extra expense or personnel. The present writer has been assembling standard emergence tables for some years and already has tables, based on twelve seasons, for *Rhabdophaga heterobia* H.Lw., the button-top midge of willows; and for *Contarinia tritici* Kirby and *Sitodiplosis mosellana* Géhin, the wheat-blossom midges (**3**). Tables based on fewer seasons are available for other species of gall midges.

In fact, an entomological phenological station is envisaged, staffed by a competent entomologist and a statistician assisted by a small field staff available for sampling and the routine work involved in breeding large numbers of insects. Such a station could be responsible to local advisory entomologists for providing them with information as to the season's standard dates (e.g. hatching, emergence, etc.) for almost any insect pest whose control is based on an exact knowledge of dates.

Table 7. *Rothamsted standard emergence table: carrot-fly and Braconid parasite: larvae and puparia collected during February and March*

*North Lincoln area*

| Week | 1936 | 1937 | 1938 | 1939 | 1940 | 1941 |
|---|---|---|---|---|---|---|
| 2– 8 Apr. | — | — | — | — | — | — |
| 9–15 Apr. | — | — | — | — | — | — |
| 16–22 Apr. | — | — | 10– 0 | — | — | — |
| 23–29 Apr. | — | — | 25– 0 | — | — | — |
| 30 Apr.–6 May | 1–0 | 2– 0 | 86– 2 | 6– 0 | 1– 0 | — |
| 7–13 May | 13–0 | 38– 1 | *173*–20 | 68– 2 | *34*–10 | 1– 0 |
| 14–20 May | *86*–4 | *154*– 9 | 26–14 | 54– 5 | 25–14 | 3– 0 |
| 21–27 May | — | 59– 6* | 12– 2 | *70*–14 | 4– 6 | *251*– 6 |
| 28 May–3 June | 1–0 | 16– 0 | 17– 1 | 36– 2 | 3– 1 | 186–26 |
| 4–10 June | 1–0 | 10– 0 | 29– 4 | 33– 1 | 13– 2 | 9–20 |
| 11–17 June | — | 8– 0 | 53– 0* | 18– 1 | 4– 0 | 4– 1 |
| 18–24 June | — | 2– 0 | 62– 3 | 8– 0 | 2– 0 | 6– 0 |
| 25 June–1 July | — | 2– 0 | 52– 0 | 29– 1 | 1– 0 | 12– 0 |
| 2– 8 July | — | 2– 0 | 19– 0 | 7– 0 | 1– 0 | 1– 0 |
| 9–15 July | — | 1– 0 | 12– 0 | 12– 0 | 5– 0 | 1– 0 |
| 16–22 July | — | 2– 0 | 11– 0 | 11– 0 | 1– 0 | — |
| 23–29 July | — | — | 10– 0 | 2– 0 | — | 2– 0 |
| 30 July–5 Aug. | — | — | 1– 0 | 4– 0 | — | — |
| 6–12 Aug. | — | — | — | — | 1– 0 | — |
| 13–19 Aug. | — | — | — | — | — | — |
| 20–26 Aug. | — | — | (1– 0 in Sept.) | — | — | — |
| Totals | 102–4 | 296–16 | 599–46 | 358–26 | 95–33 | 476–53 |

* In addition one other parasite emerged.

Table 8. *Rothamsted standard emergence table: carrot-fly and Braconid parasite: larvae and puparia collected during February and March*

*East Nottingham area*

| Week | 1936 | 1937 | 1938 | 1939 | 1940 | 1941 |
|---|---|---|---|---|---|---|
| 2– 8 Apr. | — | — | — | — | — | — |
| 9–15 Apr. | — | — | — | — | — | — |
| 16–22 Apr. | — | — | — | — | — | — |
| 23–29 Apr. | — | — | 3– 0 | — | — | — |
| 30 Apr.–6 May | — | 10–0 | 25– 0 | 12–1 | — | — |
| 7–13 May | — | 29–2 | *164*– 3 | 8–0 | *145*– 8 | — |
| 14–20 May | 6–0 | *87*–1 | 39– 5 | 16–0 | 65–49 | — |
| 21–27 May | — | 59–2 | 3– 2 | 78–2 | 10– 1 | 97– 1 |
| 28 May–3 June | — | 5–0 | 2– 0 | 109–0 | 12– 0 | *226*–21 |
| 4–10 June | — | 6–0 | 2– 0 | *120*–1 | 9– 0 | 97–23 |
| 11–17 June | — | 11–0 | 1– 0 | 56–0 | 6– 0 | 11– 3 |
| 18–24 June | — | 2–0 | 1– 0 | 57–0 | 1– 0 | 10– 0 |
| 25 June–1 July | — | 3–0 | — | 71–0 | 2– 0 | 7– 0 |
| 2– 8 July | — | 1–0 | 2– 0 | 24–0 | 1– 0 | 8– 0 |
| 9–15 July | — | 4–0 | — | 36–0 | 1– 0 | 1– 0 |
| 16–22 July | — | — | 1– 0 | 18–0 | — | 5– 0 |
| 23–29 July | — | 1–0 | — | 3–0 | — | — |
| 30 July–5 Aug. | — | — | — | 5–0 | — | — |
| 6–12 Aug. | — | — | — | — | — | 3– 0 |
| 13–19 Aug. | — | — | — | — | — | — |
| 20–26 Aug. | — | — | — | — | — | — |
| Totals | 6–0 | 218–5 | 243–10 | 613–4 | 252–58 | 465–48 |

### 6. Control

It has been known for a long while that the carrot-flies suddenly appear in large numbers, and it has now been confirmed by breeding that the vast majority are very quickly on the wing soon after emergence has begun. It is also known that there is a preovipositional period lasting nearly two weeks, in which the flies are obvious in the vicinity of where they emerged, i.e. carrot areas of the previous season. There thus appear to be two periods at which control of the carrot-fly appears possible. First, when the flies have emerged but not started to oviposit, and second, when the larvae and puparia are concentrated in the pies or clamps.

The opportunity was taken in 1941 to test the effect of watering formalin solution on soil containing larvae and puparia, chiefly the latter. One pot of material from each of the two localities was treated and three other pots from

Table 9. *Effect of watering larvae and puparia of the carrot-fly, just before emergence of the flies, with formalin solution*

| Material | No. of larvae and puparia | No. of carrot-flies emerging | No. of parasites emerging | % emergence | % parasitism |
|---|---|---|---|---|---|
| | | North Lincolnshire | | | |
| Control 1 | 221 | 120 | 18 | 62 | 13 |
| „ 2 | 223 | 185 | 22 | 93 | 11 |
| „ 3 | 201 | 171 | 13 | 92 | 7 |
| Treated with formalin | 218 | 16 | 2 | 8 | 11 |
| | | East Nottinghamshire | | | |
| Control 1 | 219 | 163 | 15 | 81 | 8 |
| „ 2 | 218 | 153 | 19 | 79 | 11 |
| „ 3 | 213 | 149 | 14 | 77 | 9 |
| Treated with formalin | 211 | 39 | 13 | 25 | 25 |

each of the two localities were kept as controls. The treated pots were each watered on 8 May, just before emergence might be expected to begin, with 40 c.c. of 1% formalin (40%) solution and then rewatered with 100 c.c. of water. The controls were watered with 140 c.c. of water. The results are shown in Table 9. It is apparent that the treatment reduced the number of flies emerging. As regards parasites, in the north Lincolnshire material some parasites may have been killed, but there is certainly no evidence of this in the material from east Nottinghamshire. There was no evidence in the day-to-day emergence figures that the formalin treatment delayed the emergence of either the flies or the parasites. If these results can be repeated and the cost is not prohibitive, the watering of the bases of carrot pies or clamps when the carrots are removed for washing in the spring should be carried out in areas where clamping is practised. It might even be economical in war time to enforce clamping and the subsequent treatment of clamp bases.

## 7. SUMMARY

1. This is the ninth paper dealing with fluctuations in insect populations collected in the field and studied in an out-door unheated insectary. The previous eight papers have dealt with various species of gall midges.

2. A satisfactory method of assessing the yearly abundance of the carrot-fly and its parasites is described. Data are given for the years 1936–41.

3. The dates of emergence of the adult flies for the same period are also given.

4. The preparation of standard tables for the dates of hatching, emergence, etc., of insect pests is discussed briefly. For this purpose the setting up of an insect phenological station is suggested. The function of such a station would be to provide local growers, through their advisers, with information as to the earliness or lateness of the season.

5. Treatment of the base of carrot clamps with formalin solution is recommended as a control.

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# ON THE MARINE MOLLUSCA OF STUDLAND BAY, DORSET, AND THE SUPPLY OF LIME TO THE SAND DUNES

By D. F. W. BADEN-POWELL

(*With* 1 *Figure in the Text*)

## 1. Introduction

The entrance to Poole Harbour, Dorset, is narrowed by two peninsulas. The northern peninsula is known as Sandbanks, and is entirely built over. Since 1933 the southern barrier to the mouth of the harbour has been known as South Haven Peninsula, and has been the site of a detailed biological survey started by Diver & Good (**2**). The present paper is a contribution to this survey, and discusses certain aspects of the environment of the plant and animal populations of South Haven Peninsula. My own field observations were made in the summers of 1927, 1929, 1930, 1931, 1933, 1934, and 1936. Unfortunately, it has not been possible to resume my work on the changing environment of this area since 1936.

Two main problems will be considered here. The first is the origin of the higher ground which forms Spur Heath and Plateau Heath,[1] a question which was raised in the discussion of Diver's paper at the Royal Geographical Society (**1**). These heaths have acted as a supply of heath vegetation with its attendant animals during the changes which have taken place in the rest of the area. The second problem is the reason for the lime deficiency in the dune sand, which has given the dunes here a plant and animal population unlike that usually expected on this formation elsewhere in Britain.

## 2. Geology and topography

The general shape and structure of the region must be described first, as these act as the background to the changes which have taken place, and which still continue, on South Haven Peninsula. The rock outcrops of the Isle of Purbeck run approximately from west to east, and are cut off abruptly by the east coast of Purbeck (**5**). South of Swanage, the Purbeck limestones run out to the coast in Durlston Bay, and form the capes of Durlston Head and Peveril Point. The vale between Corfe Castle and Swanage follows the outcrop of the Wealden sands, and their relative softness has contributed towards the erosion of Swanage Bay. North of this vale, the line of hills from Corfe Castle to Ballard Down is formed of chalk, with a narrow belt of sand and clay (Greensand and Gault) on its southern side. The chalk ridge of Ballard

[1] For local names not on the Ordnance Survey maps, see sketch-map, Fig. 1.

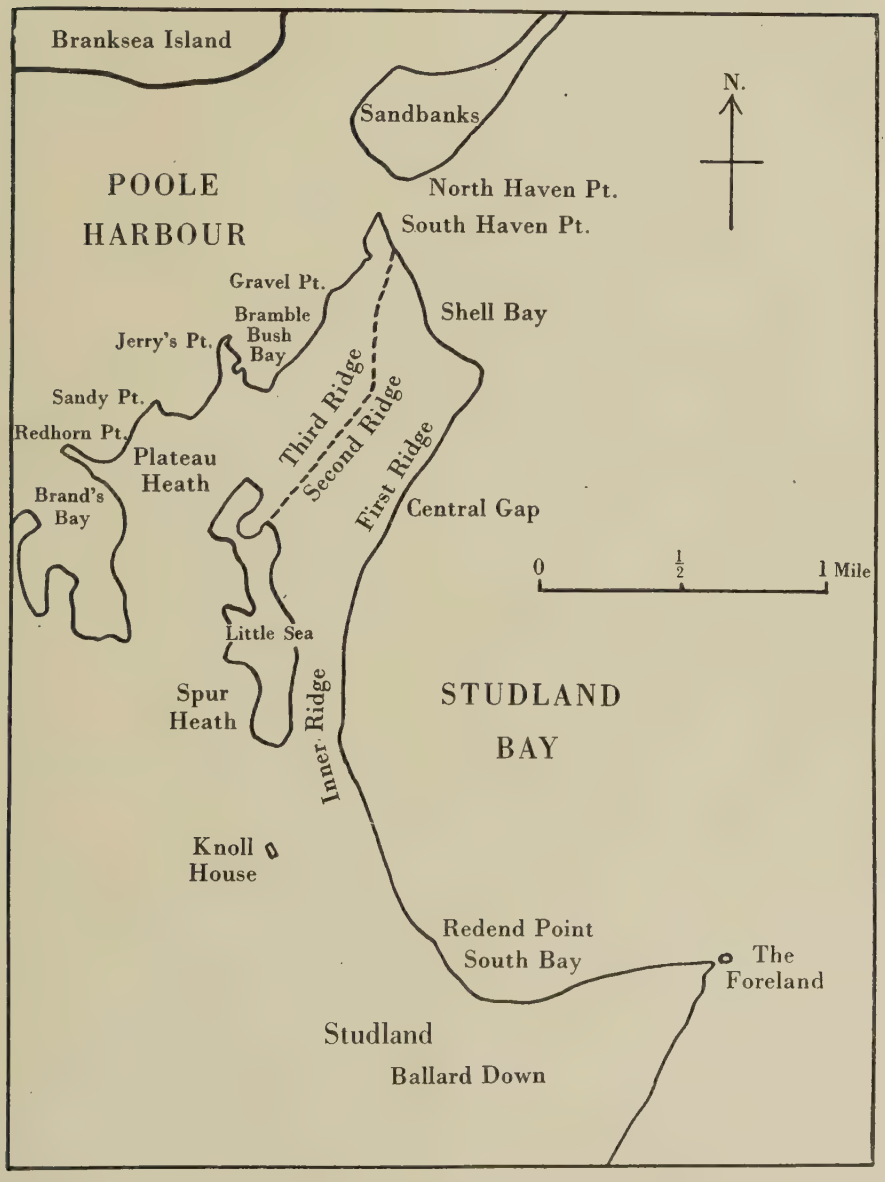


Fig. 1. Sketch-map of South Haven Peninsula and Studland Bay, Dorset.
(Broken line shows drainage ditch from Little Sea.)

Down forms the southern limit of Studland Bay, and ends in the Foreland and the sea stack known as Old Harry. This chalk has resisted marine erosion because it is extra hard and in places contains many seams of flint.

North of the chalk a narrow band of Reading Beds (Clay and ferruginous sandstone) and London Clay reaches the coast in South Bay, but does not greatly affect the topography. The country round Poole Harbour has for its foundation sands and clays of the Bagshot Beds, and although these are relatively softer than the chalk here, contributing to the formation of Studland Bay, the sand is locally hardened into a sandstone in Studland village, and is there resistant enough to form a local cliff and slight headland south of the lane down to the shore. The Bagshot Beds continue round the north side of Bournemouth Bay, and contain less clay and more sand as they are traced eastward to Boscombe and Hengistbury Head (**6**).

The geological history of Poole Harbour is complicated, but for present purposes three events in its development are important. First, during the Pleistocene, great sheets of gravel were laid down, remnants of which can be seen on Spur Heath and at a large number of similar localities all round Poole Harbour. Later, this sheet of gravel was cut into separate outcrops by the erosion of streams, including the rivers Frome and Piddle which flow into the head of Poole Harbour near Wareham and the small streams like those which flow into Brand's Bay. These streams made shallow valleys with higher ground between them, and this higher ground consisted of Bagshot Beds, sometimes capped by gravel, but sometimes the only remnant of the gravel was a 'trail' of stones in the subsoil. When the new road to the ferry across the mouth of Poole Harbour was made, one of these 'trails' of gravel was exposed in a road cutting. The third event in the evolution of Poole Harbour was a rise of sea-level (or submergence of the land, or both), which resulted in the lower seaward end of the valleys being flooded by sea water. Thus in geographical terminology Poole Harbour took on its present form as a drowned valley. The old remnants of gravel on the hills still remained, as on Spur Heath, and some became isolated by tidal water, for instance the patches on Branksea Island.

Spur Heath and Plateau Heath have always formed the nucleus on which the rest of South Haven Peninsula has been built, and during the discussion which followed Diver's paper ((**1**), p. 426), G. M. Lees asked why this nucleus 'remained above the rest of the sunken area of Poole Harbour'. In my opinion the answer, as given above, is simply that these slight hills were the areas not removed by stream erosion at a date prior to the submergence of Poole Harbour. In this way the general topography of Spur Heath and Plateau Heath can be explained, although the cause of the shape of some of the more detailed features is not yet understood.

Diver (**1**) has shown that before the year 1607 this nucleus of Spur Heath and Plateau Heath was probably much as it is to-day, but that the Little Sea and the present area of sand dunes had not yet come into existence. What is

now the western shore of Little Sea was then the east coast of the peninsula, which ended near Gravel Point. The subsequent addition of the whole area north and east of Little Sea may be summarized as follows:

*1607–1721.* Building of Third Ridge and part of Southern Heath. During this period, the west coast of the peninsula was much as it is to-day, but near the present site of Studland village the shore was much farther *east* than it is now.

*1721–1785.* Addition of part of Second Ridge on to the east side of the pre-existing peninsula. Little Sea changing from a tidal inlet with sandy floor to a brackish lagoon.

*1785–1849.* Completion of Second Ridge and the landward ridges of Southern Heath, and by 1849 First Ridge had just begun to form.

*1849–1933.* Building of First Ridge. Before the year 1900, salt water had ceased to flow into Little Sea, even during exceptionally high tide.

*After 1933.* The beginning of the new dune opposite Central Gap. Diver ((**1**), pp. 416–17) describes this as a 'hillock' colonized by marram grass (*Psamma*).

The rate of growth of this youngest dune is interesting. It is first shown on the map accompanying Diver's paper (**1**) as quite small, but its exact size had not been measured. As a basis for future comparison, I measured it in August 1934 as 110 yd. long by 22 yd. broad, and its height (by hand-level) was 7 ft. It was well colonized by *Psamma*, and really consisted of two small dunes, not quite continuous, and running due north and south. Unfortunately, I have not been able to watch its subsequent development.

The history of the sand dunes as worked out by Diver is most important. For instance, it gives a time scale by which the replacement of *Psamma* by *Calluna* can be measured, this change being complete on Third Ridge and incomplete on the landward side of First Ridge. Good (**3**) has described the plant distribution as it was prior to the year 1935. The attendant distribution of birds for 1935 and 1936 has been discussed by Lack & Venables (**4**).

### 3. Conditions on the beach

The shape of South Haven Peninsula is obviously conditioned by its coast-lines, and it is important to distinguish between the different types of coast and their relation to erosion. Even an outline map like that produced by Lack & Venables ((**4**), p. 63) emphasizes the difference in shape between the two sides of the peninsula. That bordering Poole Harbour is irregular, with Redhorn, Sandy, Jerry's and South Haven Points separating comparatively deep indentations like Bramble Bush Bay. The east coast, except for the gentle curves of Shell Bay and the bay south of Redend Point, consists entirely of the wide sweep of Studland Bay. The difference is one of origin. The outline of the Poole Harbour side is, as already explained, that of a drowned valley, the filling by tidal water of the lower part of a valley previously shaped by rivers. The curve of Studland Bay is controlled by the balance between marine erosion and the seaward growth of sand dunes which is taking place on that side.

In general, erosion is in progress at the southward end of the beaches, at least between Redend Point and the end of the road which runs from Knoll House to the sea. From a short distance north almost to Shell Bay, there is no evidence for erosion, and a slow seaward advance of the dunes opposite Central Gap has already been mentioned. In Shell Bay itself, however, erosion is again met with. I have not myself made any measurements of the rate of erosion in Shell Bay, but Diver ((**1**), p. 416) gives the rate as roughly 200 yd. in 38 years (1886–1924). This is an extreme rate for marine erosion (more than 5 yd. per annum), and may be connected with scour by the tidal current through the mouth of Poole Harbour. (This current is readily observable when crossing by the ferry to Sandbanks.)

It is clear that erosion is also going on at the southern end of Studland Bay, because the blown-sand formation of Inner Ridge meets the beach sand in a low 'cliff', about 5 ft. high. It is also interesting to remember that in or before the year 1721, low-tide mark is considered to have been $\frac{1}{4}$ mile east of its more recent position (Diver (**1**), p. 409 and Fig. 2). If the 1721 map is accurate enough for such calculations, the rate of erosion at this point would average about 2 yd. per annum.

This last estimate of 2 yd. per annum receives good confirmation from an independent enquiry of my own. At the wooden landing stage at the end of the lane down from Studland village to the sea, there could be seen in 1934 large blocks of concrete which are the remains of a ruined boathouse. (Other considerations suggest that these blocks are too large to be moved even during storms at this particular site.) Judging from its position as marked on the 1902 edition of the 6 in. map, and from information received from two residents of Studland (Mr Gibbons and Mr Payne), the boathouse became disused soon after 1902, when it was just below high-water mark. In August 1934 I measured the distance (by surveyor's tape) from the ruin to high-tide mark of that date as 55 yd., which for a period of 32 years also gives an average of 1·72 yd. per annum. Erosion affects the edge of the dunes at least as far as the point where the track from Knoll House reaches the coast, since the chalk foundations of the end of this road are washed down on to the beach in stormy weather. I do not believe that the erosion in this southern part of Studland Bay is due to tidal scour, because my own experience in swimming here at all states of the tide shows that the current is never very strong opposite the part where the erosion occurs. The cause of erosion at this point must therefore be wave action.

### 4. Distribution of shells on the beach

There are three sites on Studland Beach which one might expect to be colonized by Mollusca which live on rocks or seaweed. The first is at the extreme southern end of Studland Bay, where large blocks of chalk and ferruginous sandstone (Reading Beds) are scattered on the foreshore. *Mytilus*

*edulis* and *Balanus* were found living on these rocks, but were not common; and *Littorina littoralis* and Annelids were seen on the seaweeds near low-water mark, but on the whole the fauna here is remarkably poor. No small Mollusca, such as *Turtonia* or *Rissoa*, were observed living. The second site examined was Redend Point, which consists of rather ferruginous Bagshot Sandstone. There is a cliff here about 20 ft. high, with some beach below it, but also with a bare rock platform with rock pools. *Littorina littoralis* was living on seaweed, but no *Patella* or *Balanus* were found living on the rocks, and again no small Mollusca were seen living. Possibly a systematic biological survey of the marine animals would prove that these are not as rare as these observations suggest. The third site examined was the breakwater at the angle in the coast between Shell Bay and Studland Bay. This consisted of loosely piled large blocks of stone. There is much seaweed, but only *Balanus*, *Patella vulgata* and *Ocinebra erinacea* were seen living, and not even *Littorina* was found.

My object in making these investigations was to trace the source of the littoral shells found dead along the beach; no attempt at digging up sand-living species was made, and it would be a great addition to our knowledge of conditions on this beach if a complete survey could be carried out by a marine biologist.

Apart from these three rock sites, the whole of Studland Beach is sandy, except for subordinate shingle, which, contrary to usual experience, is concentrated near low-water mark (L.W.M.), when it is present at all. The distribution of the shingle will be referred to in more detail when sources of supply of lime to the sand dunes are discussed. Redend Point divides Studland Bay into two unequal parts. The small bay between this point and the beginning of the chalk cliffs which end in the Foreland will be referred to here as South Bay. North of Redend Point the main sweep of Studland Bay continues as far as the stone breakwater already mentioned, and the bay north-west of this is known as Shell Bay.

The distribution of shells of dead Mollusca on the sand beaches is very interesting. As a general rule they are restricted to a narrow zone along high-water mark (H.W.M.), but are also scattered over the wide area of sand between normal H.W.M. and the beginning of the *Psamma*-colonized dunes. This wide belt is presumably washed over by the sea during extra high tides, as it is not systematically colonized by land plants. There are also sporadic shells near L.W.M., but there is an obvious tendency for them to accumulate along the H.W.M. zone.

The width of this zone cannot be measured accurately, but it is usually less than 10 ft. When it is followed along the length of the beach, the density of shell occurrence is seen to be very uneven. Shells are much more numerous at H.W.M. at the southern end of South Bay than in its central or northern part. Then after passing round Redend Point, shells are still comparatively rare at the southern end of the main part of Studland Bay, but as H.W.M. is

traced northwards, they rise to a peak of frequency at the most westerly point in the curve of the shore, soon become scarcer, then increase again slightly as Shell Bay is approached.

Table 1. *Dead shells per sq. ft. at* H.W.M.

| Station | Density |
|---|---|
| South Bay, southern end of sand | 20·00 |
| South Bay, 100 yd. north of the last | 0·36 |
| South Bay, 200 yd. north | 1·11 |
| South Bay, 300 yd. north | 0·25 |
| South Bay, 400 yd. north | 0·09 |
| Immediately south of Redend Point | 0·003 |
| Immediately north of Redend Point | (estimate, about 0·10) |
| Most westerly point in curve of bay | 16·66 |
| Near Central Gap | 0·05 |
| Beginning of Shell Bay | 3·16 |

These figures were arrived at by doing shell counts on measured areas of sand surface. Only one count was done at each station, except for the most westerly point in the curve of Studland Bay, which is a mean of three counts. If more counts were done, these figures would no doubt vary, particularly after stormy weather, but in general several months' experience of this beach has shown that the points of maximum density remain constant in position, and are therefore permanent features of the shell distribution along H.W.M. in these bays.

The species identified among those washed up in South Bay, Studland Bay and Shell Bay (1927–36) are:

Anomia ephippium L.
A. patelliformis L.
Mytilus edulis L.
Chlamys opercularis (L.)
C. varia (L.)
Pecten maximus L.
Ostrea edulis L.
Turtonia minuta (Fabricius)
Cyprina islandica L.
Cardium echinatum L.
C. edule L.
Cardium ? exiguum Gmel.
Laevicardium norvegicum Gmel.
Lucina borealis (L.)
Venus verrucosa (L.)
Tapes aurea (Gmel.)
T. rhomboides (Pennant)
T. pullastra (Montagu)
T. decussatus (L.)
Donax ? vittatus (da Costa)
Tellina tenuis da Costa
Scrobicularia plana da Costa
Mactra stultorum (L.)
Spisula solida (L.)
S. subtruncata (L.)
S. truncata (Montagu)
S. elliptica (Brown)
Lutraria lutraria (L.)
Mya truncata L.
Mya ? arenaria L.
Pandora ? inaequivalvis (L.)
Pholas dactylus L.
Ensis siliqua (L.)
E. ensis (L.)
Solen marginatus (Montagu)
Dentalium ? entalis L.
Patella vulgata L.
P. depressa Pennant
Fissurella graeca (L.)
Calyptraea chinensis (L.)
Gibbula magus (L.)
G. cineraria (L.)
Lacuna crassior (Montagu)
Littorina littorea L.
L. saxatilis (Olivi)
L. littoralis L.
Rissoa ? parva (da Costa)
Crepidula fornicata (L.)
Natica ? catena (da Costa)
Velutina velutina (Müller)
Trivia europoea (Montagu)
Purpura lapillus (L.)
Nassa incrassata (Ström.)
N. reticulata (L.)
Ocenebra erinacea (L.)
Buccinum undatum L.

As is usual on beaches, a few of these 56 species were abundant, a few would be described as common, but the majority of the species were rare. A number of counts were done where shells of all kinds were most abundant, to find out the percentage of different species. These counts show that the peak in shell frequency in South Bay (see Table 1) is due to local abundance of rock-living forms, specially *Littorina littoralis*, while the peak in Studland Bay is due to local concentration of sand-living forms. The following figures refer to actual numbers of shells counted. Starting at the south end of South Bay, the counts were as shown in Tables 2 and 3.

Table 2. *South end of South Bay*

| | |
|---|---|
| Littorina littoralis | 87 |
| Nassa reticulata | 7 |
| Littorina saxatilis | 3 |
| Gibbula cineraria | 2 |
| Lucina borealis | 1 |
| | 100 |

Table 3. 100 *yd. north of the last*

| | |
|---|---|
| Littorina littoralis | 72 |
| Cardium edule | 8 |
| Nassa reticulata | 6 |
| Mytilus edulis | 3 |
| Solen marginatus | 3 |
| Spisula subtruncata | 2 |
| Gibbula cineraria | 2 |
| Patella vulgata | 1 |
| Ocenebra erinacea | 1 |
| Tapes pullastra | 1 |
| Lucina borealis | 1 |
| | 100 |

In counts where Lamellibranchs occur as well as Gastropods, separate valves were considered as individuals, except in cases where the valves are still joined. This was considered safe, as the chances against separate valves of an individual lying together on a beach after having been washed over by the waves are small. The counts were not continued in the same way as the two shown in Tables 2 and 3, because of the relative scarcity of all shells farther north in South Bay. At 200 and 300 yd. north *Littorina littoralis* still appears to be the commonest shell, but as H.W.M. is followed to the north end of South Bay, that is, just south of Redend Point, *Cardium edule* supersedes *Littorina* as most common. Actual counts were only made on one occasion in South Bay, but observation over a long period suggests that these relative frequencies in South Bay are fairly permanent.

In the main part of Studland Bay, counts of the percentage of the different species were again only found practicable at the two places of peak frequency of shells of all kinds (Table 1). Three counts were made within 350 yd. of each other at the most westerly angle of the bay, due east of the southern end of

Little Sea; two more were also made towards the north end of Studland Bay, about a mile away from the other three. The results are shown in Table 4.

The percentages in the first three columns are of samples taken approximately 100 yd. apart from each other, and as the first five places are occupied by the same species in each case, they may be taken as typical of this part of the beach as a whole. On the other hand, these three counts were made on two days (13 and 14 July 1927), and therefore do not alone give any indication of the permanence of this order. It will be noticed that *Cardium edule* is the most abundant species in every case, and that except for *Anomia* and *Mytilus*, all the five most common species are sand-living forms. The 'various species' include both sand- and rock-living Mollusca, the latter being, therefore, distinctly subordinate.

Table 4. *Studland Bay*

| | South end of Little Sea | | | Central Gap | Near Shell Bay |
|---|---|---|---|---|---|
| Cardium edule | 35 | 41 | 36 | 22 | 45 |
| Mytilus edulis | 13 | 12 | 15 | 28 | 9 |
| Spisula (various) | 11 | 13 | 9 | 12 | 12 |
| Tellina tenuis | 9 | 11 | 6 | 5 | 8 |
| Anomia ephippium | 8 | 11 | 16 | 11 | 5 |
| Solen marginatus | 6 | 1 | 5 | 12 | 2 |
| Tapes pullastra | 4 | — | — | 2 | 3 |
| Ostrea edulis | 2 | — | 2 | 4 | — |
| Pandora inaequivalvis | 2 | — | — | — | — |
| Mactra stultorum | 2 | 3 | — | 2 | 2 |
| Nassa reticulata | 2 | 2 | — | — | 1 |
| Gibbula cineraria | 1 | 2 | — | 1 | 3 |
| Chlamys varia | 1 | 1 | 1 | 1 | 1 |
| Littorina littorea | — | 1 | 1 | — | 2 |
| Buccinum undatum | — | — | — | — | 2 |
| Various species | 4 | 2 | 9 | — | 5 |

Table 5. *Studland Bay, opposite southern end of Little Sea*

| | |
|---|---|
| Ensis siliqua | 54 |
| Mytilus edulis | 28 |
| Cardium edule | 14 |
| Various species | 4 |
| | 100 |

The last two counts were done soon after the three earlier ones (15 and 19 July 1927), but their similarity to the first three shown in Table 4 strongly confirms that percentages of the most common shells remain similar along the sandy part of Studland Beach, as these last two counts are about a mile north of the others.

General experience of the beach confirms that the *Cardium*, *Mytilus*, *Spisula*, *Anomia* and *Tellina* remain constantly the most common shells. An exception was found in July 1929, when *Ensis* and much seaweed was washed up to H.W.M. opposite the southern end of Little Sea. A count showed the results given in Table 5.

This probably occurred after exceptionally stormy weather (and waves)

from the south-east, but no note of this was made at the time. It will be noticed that the *Ensis* is a different form from the *Solen* of the earlier counts.

Without dredging operations in Studland Bay or a survey by a marine biologist, it is not easy to account for the frequency of all the species in these counts, especially *Mytilus edulis*, which one would not expect to live in the sandy part of the bay, but taking a broad view of this work, three facts stand out as important:

(1) Rock-living species like *Littorina littoralis* are washed up most abundantly near a rocky habitat, at the southern end of South Bay.

(2) Sand-living species like *Cardium edule* are concentrated on the sandy part of Studland Bay.

(3) Shells are generally scarce immediately north and south of Redend Point, and the living molluscan population is also exceptionally scanty on the rocks which form this point.

The obvious conclusion is that *the dead shells in South Bay are not moved far from their original habitat, whereas those in Studland Bay are concentrated at certain points.* The most important of these concentration points in the main part of Studland Bay is due east of the southern end of Little Sea.

### 5. Lime deficiency of the sand dunes

There are two likely sources from which the sand dunes could be supplied with carbonate of lime: (1) chalk or other calcareous rocks, (2) shell fragments from the beach.

It is well known that most sand dunes near the sea contain sufficient carbonate of lime to have a marked ecological effect, primarily on the plants by which they are colonized, and also as a favourable habitat for land snails. All observers agree that the dunes on South Haven Peninsula are exceptionally lacking in lime, and therefore differ from most sand-dune areas that have been surveyed ecologically. This point was emphasized by Salisbury and Oldham in the discussion which followed Diver's paper at the Royal Geographical Society ((**1**), pp. 20–1). It was shown that even the young dunes at Studland are able to support acid heath vegetation, like older dunes elsewhere which have had their initial calcium carbonate content leached out, and that both land snails and the fresh-water Mollusca in Little Sea are much less abundant than one would have expected. Good (**3**) has confirmed the acidity of the dunes in his paper on the vegetation, while Lack & Venables (**4**) connect the absence of the skylark from the dunes with the effect of lime deficiency on the vegetation.

No systematic analyses have been published of the soils or underlying deposits of this area, but the following figures show how deficient lime is.

Salisbury has made three analyses of sand samples sent to him by Diver (MS. letter to me from Diver, 17 August 1933):

| Sample from | Carbonate |
|---|---|
| First Ridge | 0·00–0·5 % |
| Second Ridge | None detectable |
| Third Ridge | None detectable |

Good (letter, 15 January 1942) tells me that analysis of a number of soil samples from the blown sand area shows that the lime content of the dune sand is very low indeed, and generally less than 0·1 % of CaO.

From the point of view of likely sources of lime, the surrounding rock formations must be considered. Good ((**3**), p. 366) has already emphasized the acid nature of the soils overlying the Bagshot Beds, and my own experience of these deposits in the field is that they are largely non-calcareous. The obvious source of lime near Studland is chalk from Ballard Down, and, as already mentioned, large blocks of chalk fall from the cliffs here on to the beach, and pebbles of chalk occur among the sparse shingle. Two pebble counts were done on the shore below the chalk cliff (by identifying random samples of 100 adjacent pebbles), at sites several hundred yards apart from each other:

Table 6. *Pebbles at southern end of South Bay*

| Rock type | 1st count | 2nd count |
|---|---|---|
| Flint | 53 | 47 |
| Chalk | 39 | 42 |
| Ferruginous sandstone and mudstone | 7 | 7 |
| Sandstones and quartzites | 1 | 3 |
| Igneous | — | 1 |
| | 100 | 100 |

The ferruginous sandstone and the mudstone come from the adjacent Reading Beds; the origin of the quartzites and of the igneous pebble (? a gabbro) is unknown. When traced northwards, chalk pebbles are seen to occur for a short distance past where the sandy beach begins, but very soon die out altogether. No chalk pebbles are seen in the patches of shingle at Redend Point or in the layer of shingle which is found at L.W.M. at the southern end of Studland Bay itself. The latter consists almost entirely of flint, with subordinate ferruginous sandstone (presumably Reading or Bagshot Beds, or both), and small vein quartz pebbles out of these sandstones. Whether the chalk pebbles are ground to powder by attrition, and the finely divided material is washed away, or whatever the cause, it is clear that the chalk of the Foreland does not contribute chalk pebbles to Studland beach, neither does it occur in the beach sand as chalky grains. These observations were confirmed by examining the end of the track from Knoll House. The chalky foundations of the track are being eroded by the sea, but as the chalk is washed down on to the beach, it does not remain there, but seems to be washed away altogether.

The lime in most beach sands is in the form of shell fragments, which also get blown with the rest of the sand to form adjacent dunes. The beach sand at Studland is, however, made up almost entirely of quartz grains, together with a few other minerals, shell fragments being almost completely absent. The only exception to this is Shell Bay, but even here they are scarcer than usual. It has been shown that there is no lack of shells in Studland Bay, and the only explanation of lack of shell fragments is that the shells do not get broken up as much as usual on a beach. This is confirmed by the shells themselves. Naturally broken as well as entire shells occur here as on all beaches (*Mytilus edulis*, for instance, is sometimes chipped along its ventral margin, the weakest part of the shell); but the shells as a whole are remarkably unbroken, and this applies to thin shells like *Anomia ephippium* and *Tellina tenuis*, as well as to the stronger shells.

The reason suggested for the rarity of breakage in the shells is that wave action is never very strong in Studland Bay, owing to the protection of the Foreland. I have frequently noticed from the cliffs above Old Harry that quite big waves coming in from the Channel past the south-east cliffs of the Foreland at the end of Ballard Down become greatly reduced in height as the wave fronts swing round into Studland Bay. Naturally with south-easterly and easterly gales, bigger waves come in, but they are not frequent, and when they do occur the wave action is nothing like so great as on the coasts of Cornwall and parts of Scotland, for instance, where shell fragments are so abundant in the beach sands. Whether this is the main cause for the lack of shell fragments, and therefore of lime, is unknown, but it seems possible. The distribution of dead shells on the beach is also explained by this theory. South Bay being more protected than Studland Bay, with maximum exposure to the north-east, shells of *Littorina littoralis* which lived on the nearby rocks become concentrated into the most southern corner of the bay. In Studland Bay the greatest exposure is towards a point a little north of east, and the shells of the Mollusca which have lived in the nearby sandy facies become concentrated along the most westerly part of the shore, that is, opposite the southern part of Little Sea. During average weather the wave fronts in Studland Bay can often be seen focusing in this way. The waves coming from eastward first strike the point at Shell Bay and Redend Point simultaneously, and run together from north and south along the shore to meet at the 'focus' where the shells are concentrated. These observations about the wave fronts agree well with Lewis's explanation (7) of the shape of bays both here and elsewhere. He shows that many bays are orientated to face the direction from which the most active wave action approaches, and includes Studland Bay as an example.

The new breakwater running south-eastward from Shell Bay was hardly completed when my observations were made, therefore its subsequent effect on the movement of beach material is not discussed in the present paper.

During exceptionally stormy weather (for Studland), shells are certainly moved on the beach by wave action (height of wave observed up to 1 ft. 2 in.), and even stones up to 8 in. diameter have been observed to move (July 1933). Exactly why the shingle in Studland Bay is left at L.W.M. instead of being moved up to H.W.M. is not clear, but as far as the shells are concerned wave action here can be said to be strong enough to move them to points of concentration on parts of the beach, but is not strong enough to break them into small fragments.

It seems reasonable to assume that the sand which forms the dunes has been derived from the shore of Studland Bay, and, in fact, frequently sand can be seen blowing up off the beach on to First Ridge; also, as Good has noted (**3**), the surface layers are liable to movement by the wind in certain places inland among the dunes. The provenance of the beach sand itself is at present unknown, and is probably a more complicated question than might be supposed.

The important point is that if the origin of the blown sand is off Studland beach, *the lack of carbonate of lime in the dunes is due to lack of shell fragments on the beach, which in turn is due to the protection given by the Foreland to Studland beach against excessive wave action.*

## Summary

1. The frame of the Studland area consists of the chalk hills of Ballard Down to the south and the lower ground made up of Reading Beds, London Clay and Bagshot Beds surrounding Poole Harbour.

2. In Pleistocene times sheets of gravel were laid down, and these were dissected later by shallow river valleys. Later still, Poole Harbour was formed by the drowning of the seaward ends of these valleys.

3. From the seventeenth century to the present day, sand dunes have accumulated, and a fresh-water lake called the Little Sea has been evolved from what was originally a tidal beach. Thus the rate of change in the environment of the existing plant and animal population of Studland is known.

4. The dune sand is exceptionally deficient in lime, a factor which strongly affects the plant and animal distribution.

5. The lack of lime is considered to be due to lack of shell fragments being blown from Studland beach, and the lack of shell fragments is certainly not due to lack of marine Mollusca in Studland Bay, and is therefore attributed to the fact that Studland Bay is exceptionally sheltered from strong wave action, and therefore the shells on the beach do not get broken by the waves as much as on a normal beach.

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# FLUCTUATIONS IN NUMBERS OF THE MUSKRAT (*ONDATRA ZIBETHICA*) IN CANADA

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(*With* 21 *Figures in the Text*)

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## 1. Introduction

Much attention has been given during the last twenty years to the ten-year cycle in forest fur-bearing animals in Canada, and its effects upon the fur trade and upon wild life generally. We know that this cycle, whose average length is slightly less than ten years, is most clearly shown in the fur returns of the lynx (*Lynx canadensis*), which prove it to have been in existence since the eighteenth century; and in the abundance of the snowshoe rabbit or varying hare (*Lepus americanus* and allied species), which is the main controlling factor of the lynx fluctuations. It also appears in the Canadian fur returns of coloured fox (*Vulpes fulva*, etc.), coyote (*Canis latrans*), wolf (*Canis lupus*), marten (*Martes americana*), fisher (*Martes pennanti*) and some other terrestrial fur-bearers—at any rate for certain districts and periods of years; and among game birds such as the ruffed grouse (*Bonasa umbellus*), and raptorial birds such as the goshawk (*Astur atricapillus*) and the great horned owl (*Bubo virginianus*).

There is no doubt that the cycles are real ones in these populations and not simply the result of market or trapping variations; that they are widespread among different terrestrial species of the forest zone (especially in the northern conifer belt); that they often happen over enormous tracts of country; and that there is a tendency for the years of abundance and scarcity to

synchronize regionally. For these reasons it has been suggested (Elton, 1924, 1925, 1929) that some climatic factor must be invoked to explain the broad integration of these scattered and ecologically diverse populations into a common rhythm of numbers. There are, however, loopholes in this theory, that have led other people to look for purely ecological relationships within the community of animals and plants to explain the cycle (as Green—in Elton and others, 1933, p. 18). These are thought of as vast periodic pandemics of disease, or mortalities caused by other pathological conditions such as the over-eating of their food supplies by herbivorous species, or of their herbivorous prey by carnivorous species, or by the interaction of all these factors. It is known, indeed, that many predatory animals (wolf, lynx) and raptorial birds (goshawk) perform large movements in search of abundant food, and so might exert a unifying effect upon fluctuations in widely separated populations. The interest aroused in recent years by the mathematical theories of Lotka and of Volterra about interspecific oscillations in numbers has doubtless turned the minds of ecologists in this direction. Against this type of argument it may be said that the total numbers and the scale of movements of these migrant or nomadic predators (especially in the comparatively reduced state of their numbers in modern times) are insufficient to bring about such control; and that the only really thorough work yet done upon the causes of disease in snowshoe rabbits during the decline of their cycle (by Green and his associates in Minnesota—see Green and others 1939), has not disclosed virulent parasitic disease in pandemic form, but a widespread and peculiar mortality from nutritional or other physiological disturbances.

The most serious argument against the climatic theory is that no one has yet been able to point to any direct meteorological evidence for a climatic cycle of the right length to account for the population rhythm. Although, in view of the sparsity of earlier Canadian weather records taken in a standard manner, and the well-recognized inapplicability of most standard meteorological instrumental readings to the life of mammals and birds, this is by no means a final argument, it is obviously a very just one.

The supposed correlation with the sunspot cycle, with its average period of about 11 years, originally suggested by Elton in 1924, but subsequently abandoned by him after studying the fuller records of the Hudson's Bay Company, has also been carefully analysed by MacLulich (1937), who gives a satisfactory disproof of the correlation. This sunspot hypothesis was originally attractive because the length of cycle was rather close to that in the lynx and rabbit and because it offered a possible clue to climatic cycles of the same length. But the sunspot hypothesis (for as such it was originally stated) has rather attracted attention away from other aspects of the question, and has been uncritically accepted by quite a large number of biologists. We are therefore still faced with an unresolved conflict of evidence, since there is no climatic cycle yet known of the right length to explain a population cycle

that cannot be entirely accounted for by any combination of other causes. It is not very difficult to imagine how there might be rhythms in numbers brought about by purely biological factors, but it is extremely difficult to explain why they should tend to synchronize over such enormous stretches of country in the same years.

The present study of muskrat fluctuations in the muskrat or musquash (*Ondatra zibethica*) provides some further support for the existence of a climatic factor influencing the ten-year cycle, for it shows that a cycle of this length also exists in an aquatic animal which is not known to have much direct ecological connexion with the terrestrial species having the same cycle.

These muskrat fluctuations, whatever their cause, have a considerable economic importance in the fur trade. Muskrat skins form the most valuable fur crop that is trapped wild in Canada at the present day, though silver fox and mink fur farming in recent years have sent up the total value of each of these species above that of the muskrat. Here are some typical figures for Canada for the year 1937–8, from the Dominion Bureau of Statistics reports:

| | No. of skins | Value ($) |
|---|---|---|
| Silver fox (wild and farmed) | 275,541 | 6,183,522 |
| Mink (wild and farmed) | 139,740 | 1,400,587 |
| Muskrat (wild; farm numbers negligible) | 1,748,239 | 1,320,509 |

(This was not a peak year for muskrats: in 1932–3 there were 2,731,490.)

## 2. Previous work and acknowledgements

The first person we know to have pointed out the existence of a ten-year cycle in the muskrat fur returns of the Hudson's Bay Company was Innis (1927), in a book dealing with the economic aspects of the Canadian fur trade, based partly on unpublished theses by his students (P. E. Salter, in the chapter concerned). The figures used by him had been published by Jones in 1914. Hewitt, in his classical summary (1921, ch. 9) of the ten-year cycle in Canadian fur-bearers, did not give any fur returns for the muskrat, though he mentioned that it was subject to fluctuations. The curve for muskrat furs published by Seton (1912, p. 107) bears no resemblance to the fur sales, and it is not clear to what region his figures refer.

In 1928 Elton began analysing some recent fur returns and earlier sales statistics of the Hudson's Bay Company, which could not at that time be published. Reference was made by him to the existence of a ten-year cycle in muskrat furs, at the Matamek Conference on Biological Cycles, in Canada in 1931 (Elton and others 1933, p. 19). Information has also been accumulated since 1925 through the annual zoological reports of the Company's fur post managers, and since 1933 from an investigation of the Company's older archives in London. During this work on the archives considerable assistance was also given by Mrs Phoebe Jackson. The Governor and Committee of

the Hudson's Bay Company have taken a generous attitude towards the publication of materials for scientific record.

This prolonged research has been aided by grants from the Hudson's Bay Company; New York Zoological Society; the Leverhulme Research Fellowship Trust; the Christopher Welch Trust; Oxford University; Corpus Christi College, Oxford; the Department of Scientific and Industrial Research; and the Carnegie Corporation of New York (through the Carnegie Institution of Washington). Valuable help has been received from a great many people, including officials of the Hudson's Bay Company, whom it is not possible to thank individually.

### 3. Fur returns of the Northern Department of the Hudson's Bay Company, 1821–1913

We have the fur returns of the Northern Department of the Hudson's Bay Company by separate fur-trade districts from 1821 to 1913, except for the years 1892–6, the figures for which have not been traced, except in the case of MacKenzie River District. (The 'year' adopted here is explained at the beginning of § 4.) This great Department covered what are now the three Middle West provinces of Alberta, Saskatchewan and Manitoba, as well as the MacKenzie River basin in the Northwest Territories, and part of Western Ontario.

The main geographical area covered by this Department did not alter much during the nineteenth century, though there were fluctuations in the exact position of its limits. Of these, three are important. First, the outer boundary of the MacKenzie River District was extended into the mountains (1842–52), and later into the head waters of the Yukon River basin (1846–92). Secondly, the southern parts of the Middle West became gradually settled and farmed, more especially after the middle of the century, and this caused a gradual decrease in the contribution of furs from these areas, and eventually (during the present century), a complete withdrawal of the Company's fur posts from the prairie and grove belts. This change and the penetration of new country gradually shifted the main incidence of trapping northwards, but without causing any sudden disturbance in the total fur returns from year to year. The third variation occurred in the eastern and north-eastern boundary of Lac la Pluie District, which lay mainly in the western end of Ontario. This District lost and gained posts in certain years, exchanging with the Albany District of the Southern Department. We think it unlikely that any of these three fluctuations in the limits of the Northern Department invalidate the conclusions drawn here from its total fur returns.

The number of districts into which the Department was divided changed from time to time, and there are fewer now than formerly (e.g. 11 in 1821, 14 in 1891, 5 in 1901, with variations in between these dates). We also have some fur returns for the Southern, Montreal and Western Departments, which made up the rest of the Hudson's Bay Company's trading territory; but there is not a long or complete enough run of years to contribute much to the muskrat analysis.

The total muskrat furs taken in the Northern Department are given in Table 1 and Fig. 1. They are copied from old account books in the London Archives of the Company. The series 1821–91 was copied from totals given; those for 1897–1913 were added up from separate districts. (There are no figures for Winnipeg in 1903, 1904, 1909 and 1910.) They show the following features: (*a*) very great fluctuations all through the period, e.g. from 170,788 in 1824, up to 936,600 in 1828, and down to 128,602 in 1830; from a peak

Table 1. *Fur returns of muskrat, Northern Department, Hudson's Bay Company Outfits* 1821–91 *and* 1897–1913. *Figures for Winnipeg missing from* 1903, 1904, 1909 *and* 1910 *totals*

| | | | | | |
|---|---|---|---|---|---|
| 1821 | 302,444 | 1851 | 383,306 | 1881 | 902,606 |
| 1822 | 345,620 | 1852 | 432,484 | 1882 | 918,960 |
| 1823 | 317,685 | 1853 | 236,925 | 1883 | 809,167 |
| 1824 | 170,788 | 1854 | 152,989 | 1884 | 454,241 |
| 1825 | 264,724 | 1855 | 188,820 | 1885 | 255,586 |
| 1826 | 399,196 | 1856 | 199,275 | 1886 | 273,673 |
| 1827 | 723,927 | 1857 | 148,900 | 1887 | 131,554 |
| 1828 | 936,600 | 1858 | 95,427 | 1888 | 192,790 |
| 1829 | 681,502 | 1859 | 125,983 | 1889 | 483,606 |
| 1830 | 128,602 | 1860 | 217,080 | 1890 | 596,382 |
| 1831 | 243,506 | 1861 | 267,656 | 1891 | 847,540 |
| 1832 | 364,256 | 1862 | 294,345 | 1892 | Records missing |
| 1833 | 578,074 | 1863 | 233,156 | 1893 | |
| 1834 | 554,848 | 1864 | 168,931 | 1894 | |
| 1835 | 218,346 | 1865 | 156,981 | 1895 | |
| 1836 | 234,499 | 1866 | 148,544 | 1896 | |
| 1837 | 302,642 | 1867 | 177,392 | 1897 | 566,157 |
| 1838 | 249,702 | 1868 | 194,670 | 1898 | 553,172 |
| 1839 | 225,224 | 1869 | 227,398 | 1899 | 747,687 |
| 1840 | 215,577 | 1870 | 427,272 | 1900 | 1,262,018 |
| 1841 | 222,589 | 1871 | 480,697 | 1901 | 1,360,086 |
| 1842 | 251,691 | 1872 | 522,818 | 1902 | 910,294 |
| 1843 | 155,946 | 1873 | 395,563 | 1903 | 792,042 |
| 1844 | 148,848 | 1874 | 410,515 | 1904 | 468,274 |
| 1845 | 203,915 | 1875 | 366,818 | 1905 | 298,252 |
| 1846 | 174,159 | 1876 | 298,590 | 1906 | 133,097 |
| 1847 | 152,423 | 1877 | 377,047 | 1907 | 254,327 |
| 1848 | 111,914 | 1878 | 357,517 | 1908 | 481,758 |
| 1849 | 106,384 | 1879 | 591,703 | 1909 | 808,449 |
| 1850 | 216,055 | 1880 | 946,526 | 1910 | 700,917 |
| | | | | 1911 | 824,520 |
| | | | | 1912 | 941,855 |
| | | | | 1913 | 373,283 |

of 946,526 in 1880, down to 131,554 in 1887, and up again to 847,540 in 1891; (*b*) rather irregular fluctuations from 1821 to 1848; (*c*) more regular fluctuations from 1849 to 1913, with a conspicuous major cycle of about ten years (continued, as will be shown, in the later returns, the reports from posts, and the Dominion fur records, up to the present time). In the first part of the nineteenth century there was, therefore, no regular ten-year cycle in these fur returns, but there was a definite one during the next 60 years.

There are two possible reasons for the irregularity of the earlier period: the cycle may have been absent or not dominant in the muskrat populations

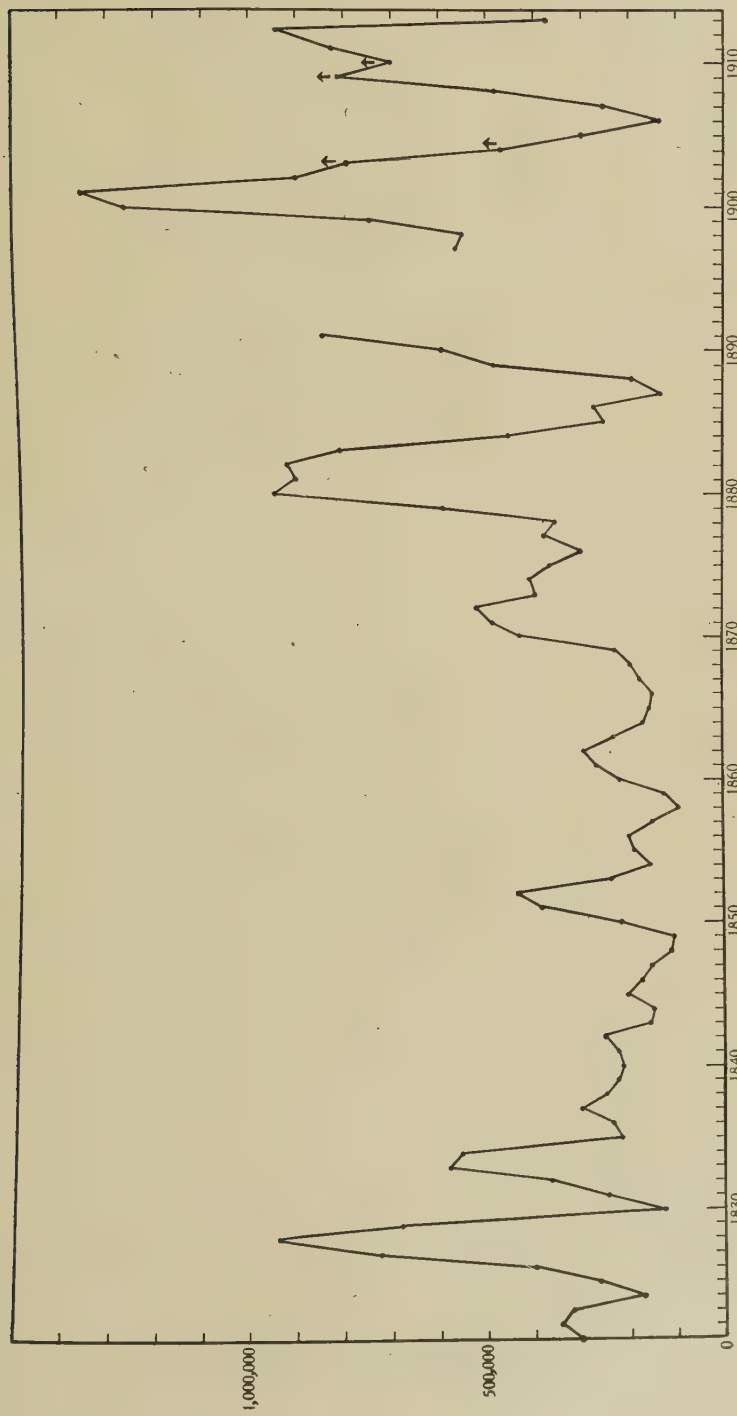


Fig. 1. Fur returns of muskrat, Northern Department, Hudson's Bay Company, Outfits 1821–91 and 1897–1913. Figures for Winnipeg missing from 1903, 1904, 1909 and 1910 totals.

themselves; or it may have been present, but not reflected in the fur returns. We have no independent evidence to tell us whether there was a natural cycle then or not, though possibly the archives for some of the important muskrat posts such as Cumberland House would produce contemporary remarks on the subject, as we have found for the snowshoe rabbit in the MacKenzie River District. On the other hand, there are strong reasons for supposing that the trade practices in this early period must have made the muskrat fur returns a poor index of natural fluctuations.

Innis (1930, pp. 332–3) states that after the absorption of the North-west Company by the Hudson's Bay Company in 1821, and during the almost complete monopoly that followed, the Company (under Governor George Simpson's policy) deliberately controlled the amount of muskrat trapping to some extent, by varying the tariff rates of bargaining with the trappers (still at that time reckoned in terms of 'Made Beaver'). Muskrats are a bulky fur, and in those days furs came out of the country by long and difficult canoe voyages. They were also a cheap fur, and indeed still are relatively so in spite of very great increases in value. These tariff changes were, according to Innis, applied much more sweepingly to muskrat than to fine furs such as the lynx and marten (which show a clear cycle even in these early years). In 1839, for instance, muskrat prices were reduced all through the Northern Department. Sometimes (as in 1841 and 1842) only muskrats caught in the spring were to be accepted at the posts. Innis sums the situation up by saying: 'Monopoly control was effective in controlling the production and sale of the cheaper furs as in the case of the muskrat....The tariff was a mechanism by which the Company was able to carry out its policies of conserving furs, in controlling the supply marketed, and in making the largest possible returns. Its effectiveness was seriously impaired with increase in trade from the south and the weakening of the Company's monopoly position.'

The Company's monopoly over Rupert's Land (which covered a large part of the Northern Department) ended in 1869; but no doubt the effects of competition were felt, at any rate in some places, before that date, if not directly, at any rate indirectly through the position in districts outside the Department. We do not know at what point the practice of varying tariffs ceased, but it was certainly bound up greatly with the monopoly period, and when competition, and later, rising prices, made the pressure on muskrat populations more heavy and continuous, the fur returns began to show more regular periodic fluctuations, though the average amounts obtained have changed gradually with the depletion of some supplies, and the capture of others by competitors. We propose, therefore, to assume that the fur returns before 1849 are unreliable as an index of population cycles (bearing in mind that their irregularities *may* possibly reflect real differences in population movements) and to confine this analysis to the years from 1849 onwards.

Owing to the gap in records from 1892 to 1896, the position of the peak which appeared to be developing by 1891 cannot be exactly placed for the Northern Department as a whole. But there are some local indications from two areas within it. There is a series of Annual Reports on Fur Trade which covers the years 1888–1928. These have been abstracted for information about fur cycles. Usually, each fur-trade district has a separate report, though these are not equally rich in fluctuation notes. There is rather little about muskrat numbers in the gap years, but notes from Cumberland District make it quite clear that the numbers of muskrats (which we know to have been rising high there by 1891) fell off considerably in the season of 1892. By 1901 this district had become incorporated in an enlarged Saskatchewan District: that year there was great muskrat abundance at the posts of Cumberland House, the Pas, and Cedar Lake, but by 1902 the numbers had fallen off. These notes suggest that in 'Cumberland District' (one of the richest muskrat-producing areas in the Northern Department) peaks may have been reached in 1891 and 1901.

We have a practically complete series of fur returns for MacKenzie River District for the years 1821–1927.

This has been constructed as follows. The Northern Department account books supply 1821–91 and 1897–1913. We have also a list of furs from the District complete for 1863–1927, supplied to Elton in 1928 by Mr Charles French, while Fur Trade Commissioner of the Company. Mr French said that these figures were obtained from private records kept by some of the older fur-trade factors. They are not identical with those in the other series, the discrepancies being apparently due to a particular set of posts having been selected to provide a 'standard district' throughout the period. Judging from the 1915–27 figures, these posts were Forts McPherson, Good Hope, Norman, Simpson, Liard, Nelson, Providence, Rae and Resolution. As the discrepancies are not very large, we have used Mr French's list to fill the gap in 1892–6, his figures for 1890–1 and 1897–1913 being identical with those for these posts in the account books. The 1914 figure is taken from the Annual Report on Fur Trade for that year (consulted in the Company's London archives). Figures for 1908–13 in earlier Reports agree exactly with those from the old account books. From 1915 to 1927 we have used the detailed fur returns supplied by the Company's Winnipeg office. The area we have taken for comparison with the pre-1915 figures is the MacKenzie River District south to and including Fort Resolution. That is to say, we omit recent extensions southward into what was in earlier days part of the Athabasca District.

The figures are given in Table 2 and illustrated in Fig. 2. The 'ten-year' cycle is very plain after about 1866, with peaks in 1870, 1878–9, 1889, 1899–1900, 1909 and 1921. This illustrates the cycle shown by a fairly homogeneous large district within the Northern Department.

A breakdown analysis of the Northern Department muskrat fur returns into separate regions will not be given here, as the main object of the present paper is to show the existence of a general ten-year cycle in muskrats, without going into a detailed regional analysis for early years.

To sum up: The Northern Department as a whole after 1849 had peaks in 1852, 1862, 1872, 1880 (probably around 1890), 1901 and about 1912. The

Table 2. *Fur returns of muskrat, MacKenzie River District, Hudson's Bay Company, Outfits* 1849–1927 (*for limits of district in different years, see text*)

| | | | | | |
|---|---|---|---|---|---|
| 1849 | 41,220 | 1879 | 20,501 | 1909 | 52,850 |
| 1850 | 33,645 | 1880 | 14,114 | 1910 | 44,792 |
| 1851 | 31,007 | 1881 | 10,408 | 1911 | 41,477 |
| 1852 | 22,264 | 1882 | 7,307 | 1912 | 39,144 |
| 1853 | 47,007 | 1883 | 5,889 | 1913 | 19,659 |
| 1854 | 15,555 | 1884 | 9,328 | 1914 | 10,328 |
| 1855 | 14,091 | 1885 | 8,469 | 1915 | 14,313 |
| 1856 | 18,122 | 1886 | 5,684 | 1916 | 683 |
| 1857 | 18,335 | 1887 | 12,110 | 1917 | 23,741 |
| 1858 | 22,720 | 1888 | 21,354 | 1918 | 45,651 |
| 1859 | 25,332 | 1889 | 40,496 | 1919 | 60,571 |
| 1860 | 17,614 | 1890 | 28,965 | 1920 | 81,409 |
| 1861 | 17,247 | 1891 | 10,612 | 1921 | 120,615 |
| 1862 | 12,996 | 1892 | 11,148 | 1922 | 115,782 |
| 1863 | 18,751 | 1893 | 11,381 | 1923 | 68,257 |
| 1864 | 11,182 | 1894 | 11,931 | 1924 | 58,273 |
| 1865 | 6,976 | 1895 | 10,289 | 1925 | 42,129 |
| 1866 | 10,457 | 1896 | 12,315 | 1926 | 60,865 |
| 1867 | 5,024 | 1897 | 10,369 | 1927 | 65,378 |
| 1868 | 9,399 | 1898 | 15,653 | | |
| 1869 | 19,347 | 1899 | 19,956 | | |
| 1870 | 27,172 | 1900 | 19,621 | | |
| 1871 | 12,828 | 1901 | 15,350 | | |
| 1872 | 3,417 | 1902 | 8,107 | | |
| 1873 | 5,069 | 1903 | 8,815 | | |
| 1874 | 7,201 | 1904 | 3,128 | | |
| 1875 | 7,761 | 1905 | 3,175 | | |
| 1876 | 11,218 | 1906 | 5,766 | | |
| 1877 | 18,380 | 1907 | 8,910 | | |
| 1878 | 20,928 | 1908 | 36,866 | | |

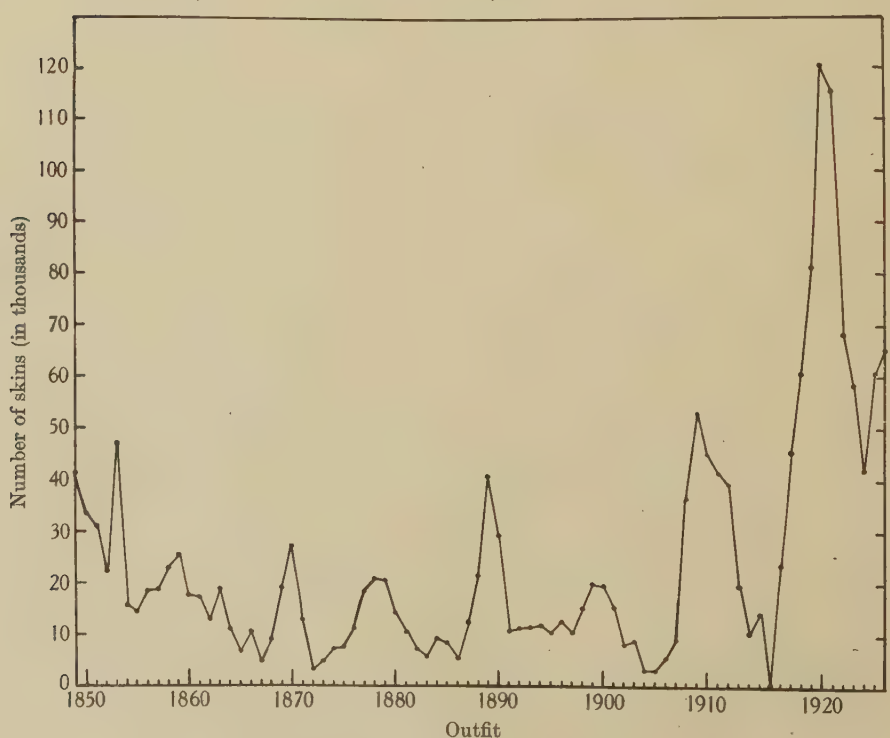


Fig. 2. Fur returns of muskrat, MacKenzie River District, Hudson's Bay Company, Outfits 1849–1927.

minimum years were in 1849, 1858, 1866, 1876, 1887 (around 1898?), and 1906. The doubtful years in the nineties are confirmed in a general way by the sales figures.

### 4. Fur sales of the Hudson's Bay Company, 1853–1911

Poland (1892, p. lvi) states that the sales of muskrat skins by the Company in London were held in January each year. It appears that the modern practice of holding autumn muskrat sales in the same year that furs were received did not start until 1915 or after (information from Company officials), so that the year given for sales up to 1911 was two years after that of the Outfit year in which they would be given in the fur returns. For instance, stores sent out to the districts in the summer of 1890 were counted as Outfit 1890 (which ran from June 1890 to May 1891). The furs of this Outfit were collected during the winter of 1890–1, sent home in the summer of 1891 (Outfit 1891), and sold early in 1892. But these sales are always listed by the Company under the calendar year (here 1892), not their *Outfit* year (here 1891).

We shall assume, on the basis of statements received from Hudson's Bay Company officials in 1928, that usually no serious 'holding' of furs took place since about 1860, i.e. that all furs received in England each year were put up and sold at auction during the following year. But the fact that the Northern Department's total muskrats for 1884 (454,241) is greater than the corresponding total sales for 1886 (347,050)—a discrepancy of at least 107,191 skins, or 24%—suggests that this policy was not invariably adhered to.

There is another disturbing factor, which Poland points out (pp. xxvi, xxvii). In a few years, some of the furs failed to reach England at the usual time, or were lost:

1864. Moose River and Eastmain Districts (Southern Department) furs did not arrive, and were sold in 1865.
1873. Ditto, sold in 1874.
1884. Ditto, but the usual furs of 1885 for these two districts were lost at sea.
1886. Part of the York Factory District (Northern Department) furs were not imported, owing to wreck of a boat, but came in 1887.
1890. Part of York Factory furs not imported.

Information for more recent years is not available, but it may be assumed that deliveries must have become, on the whole, more certain (except for some changes during the War of 1914–18, which do not affect the period under discussion).

The total output of muskrat furs at Moose River and Eastmain Districts from 1852 to 1875 (records for 1863 and 1864 missing), was never more than 26,000 skins per year. That of York Factory District for 1886 was 257, and for 1890 was 31,649. We may safely conclude that the effect on total sales of such accidents of delivery was negligible during the period 1860–1911. No other delays or losses are noted by Poland for the years 1821–92, except that the furs of Moose River and York Factory Districts for 1833 (Moose River unknown; York Factory, 1883 skins) were delayed one year; also those of York Factory District of 1836 (308 muskrats). This removes any possibility of serious disturbance from

such causes in the Northern Department returns analysed in § 3. There were, however, a few small items (not mentioned by Poland) which usually took two years instead of one to be collected and to reach the coast of Hudson's Bay. Such were the Yukon contributions of the MacKenzie River District years of Outfits 1847–69. These small items cannot, however, have seriously influenced the total fluctuations shown.

The fur sales figures for 1860–1911, from Jones (1914), are given in Table 3 and Fig. 3. These are the ones reproduced on a graph by Innis (1927, p. 36), who remarks: 'Muskrat accordingly has a cyclical production of approximately ten years....The high points of production occur, however, at points of low production for lynx and other animals.' He was inclined to attribute the cycle to the combined effects of a real cycle in numbers with a periodically increased trapping caused by the corresponding cyclical scarcity of more valuable furs. His graph also shows the price fluctuations (adjusted to allow for changes in the prices of wholesale goods generally). There is a distinct inverse correlation; also a great average increase in prices after 1905. This point will be referred to in § 5.

The sales for 1853–9 are taken from a published Report of the Company (1878) which gives sales of all furs for the years 1853–77. The section overlapping with the returns given by Jones (years 1860–77) agrees as regards the muskrats, except for one very small discrepancy of 90 skins in 1861.

Elton had in 1928 independently noticed this ten-year cycle in muskrat sales figures supplied by the Company. The sales figures published by Poland do not agree at all closely with those given to Jones by the Hudson's Bay Company, with those in the Report mentioned above or with those supplied in 1928. It seems that Poland's figures are not reliable, which is unfortunate, as they go back as early as 1752. The general authenticity of Jones's figures for muskrat sales is confirmed by some mentioned by MacFarlane (in Mair, 1908, pp. 244–5), who was at one time a chief factor in the Company's northern districts. He was an exceptionally gifted fur trader and naturalist. All his definite figures agree, except two, which are close. Such discrepancies, where they are not gross, are to be explained as different stages of the accounting sequence, due to such things as the discarding of skins of originally poor quality, or of those spoiled for any reason during transit, and the occurrence or correction of accounting errors.

In the following discussion we shall refer to the real Outfit years represented by sales years, as they are shown on Fig. 3, where they are plotted as 'sales year minus 2'. The curve does not show a very regular fluctuation until about 1867, after which several major cycles can be distinguished with peaks in 1871, 1880–2, 1891, 1894, 1900, and minima in 1868, 1875, 1887, 1895, 1906. Some sales figures corresponding to the Outfit years 1910, 1911 and 1912 have been read off from a graph in the Hudson's Bay Company's London records as 1,005,000, 960,000 and 1,003,000. This graph, though known to be not wholly reliable as a record of total sales, is probably good enough to

show that very high sales were again reached in these three years. The 1913 furs were not sold in England, owing to the War in 1914. As will be seen in

Table 3. *Sales of muskrat furs by the Hudson's Bay Company*, 1853–1911 (*from Jones*, 1914). *Dates are actual years of sale*

| | | | | | |
|---|---|---|---|---|---|
| | | 1871 | 443,999 | 1891 | 574,742 |
| | | 1872 | 704,789 | 1892 | 806,103 |
| 1853 | 493,952 | 1873 | 767,896 | 1893 | 934,646 |
| 1854 | 512,291 | 1874 | 671,982 | 1894 | 648,687 |
| 1855 | 345,626 | 1875 | 523,802 | 1895 | 674,811 |
| 1856 | 258,806 | 1876 | 583,319 | 1896 | 813,159 |
| 1857 | 302,267 | 1877 | 437,121 | 1897 | 551,716 |
| 1858 | 313,502 | 1878 | 486,030 | 1898 | 568,934 |
| 1859 | 254,246 | 1879 | 499,727 | 1899 | 701,487 |
| 1860 | 177,291 | 1880 | 478,078 | 1900 | 767,741 |
| 1861 | 206,020 | 1881 | 829,034 | 1901 | 928,199 |
| 1862 | 335,385 | 1882 | 1,029,296 | 1902 | 1,650,214 |
| 1863 | 357,060 | 1883 | 1,069,183 | 1903 | 1,488,287 |
| 1864 | 509,769 | 1884 | 1,083,067 | 1904 | 924,439 |
| 1865 | 418,370 | 1885 | 817,003 | 1905 | 1,056,253 |
| 1866 | 320,824 | 1886 | 347,050 | 1906 | 695,070 |
| 1867 | 412,164 | 1887 | 380,132 | 1907 | 407,472 |
| 1868 | 618,081 | 1888 | 344,878 | 1908 | 172,418 |
| 1869 | 404,173 | 1889 | 223,614 | 1909 | 302,195 |
| 1870 | 232,251 | 1890 | 322,160 | 1910 | 749,142 |
| | | | | 1911 | 963,597 |

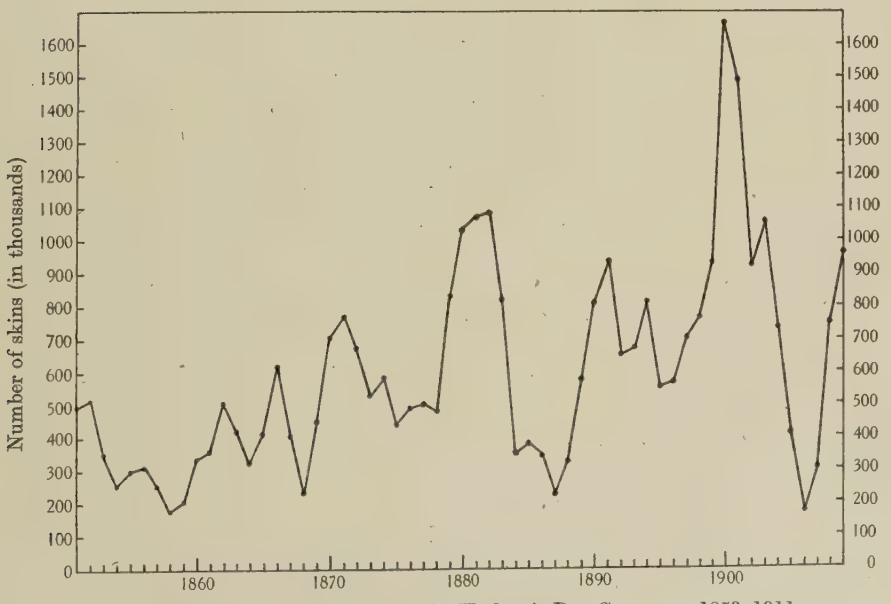


Fig. 3. Sales of muskrat furs by the Hudson's Bay Company, 1853–1911. Dates are 'sales years minus 2'.

§ 5, the numbers were low by 1915. It is reasonable to place the peak within the years 1910–12. We have therefore five main 'ten-year' cycles between 1867 and 1912, the one in the nineties being strongly interrupted in 1894.

Unfortunately, the absence of fur returns for 1892–6 prevents us from knowing whether this peak was caused by Northern Department or other furs; but there is a slight suggestion of its presence in the MacKenzie River District returns.

When the Northern Department fur returns are subtracted from the total sales (putting the latter two years back), the resulting curve shows no pronounced cyclical regularity at all, there being very high years in 1866, 1870–1, 1900, 1908 and 1910, with many smaller fluctuations between (comparison has to omit the gap in 1892–6). This irregularity proves that the Northern Department furs were the main regular cause of the ten-year component in the sales fluctuations, and that the areas outside it, taken as a whole (i.e. the Southern, Montreal and Western Departments, covering much of the rest of Canada) were not dominated by it. The percentage of the total contributed by these areas reached 76% in 1866, but more frequently fluctuated in the region below 45% and once even fell to zero. It does not follow that in these outside areas there were not some districts that had the ten-year cycle: in fact it will be seen in § 6 that some of them do have it now.

### 5. Fur returns of the Hudson's Bay Company, 1915–27

In 1928 a rather full analysis was made of the fur returns of all the Company's posts for Outfits 1915–27. (We shall here retain, for convenience of comparison, the Outfit notation of earlier years, although for trading reasons the Company now uses a different system in which the season 1927–8 for instance, corresponding to the old Outfit 1927, is called Outfit 258, in a series dating from the foundation year of the Company in 1670.)

In these returns we need to distinguish between the regular collections at ordinary posts and the activities of special cash-buying centres situated in the more closely settled regions such as the southern Middle West. The collections at the former were not influenced much by short-term market fluctuations, though strongly by competition from free traders in many places. The quantities of the cash-bought furs were dependent on policies in particular years. The total fur returns from all posts, after eliminating cash-buying agencies, are shown in Table 4 and in Fig. 4. They show a remarkably smooth cycle rising from low numbers in 1915 to a peak in 1921–2, and falling low again by 1927. This curve essentially corresponds to the total sales of the Company in previous years, when cash buying was on a relatively smaller scale or absent.

The individual posts show this cycle to a remarkable extent, considering that they are often subject to competition or other local factors influencing the collections. The curves for all posts that had complete runs of figures for the whole or nearly the whole period of 12 years were examined individually. Of these 120 posts, a large proportion showed a quite simple curve with no

irregularities or minor fluctuations. Those showing such irregularities were treated by the arbitrary method of smoothing in successive three-year means $\left(\frac{a+b+c}{3}\right)$, in order to reduce any masking of the longer cycle. If after this a curve lost its minor irregularities it was classified with the first lot as 'smooth'.

Table 4. *Total fur returns for muskrat, Hudson's Bay Company, Outfits* 1915–27, *excluding those from cash-buying agencies*

| Outfit | Fur returns | Outfit | Fur returns | Outfit | Fur returns |
|---|---|---|---|---|---|
| 1915 | 147,729 | 1920 | 555,434 | 1924 | 325,409 |
| 1916 | 166,420 | 1921 | 724,999 | 1925 | 280,447 |
| 1917 | 194,013 | 1922 | 710,921 | 1926 | 274,067 |
| 1918 | 289,014 | 1923 | 458,687 | 1927 | 290,874 |
| 1919 | 416,954 | | | | |

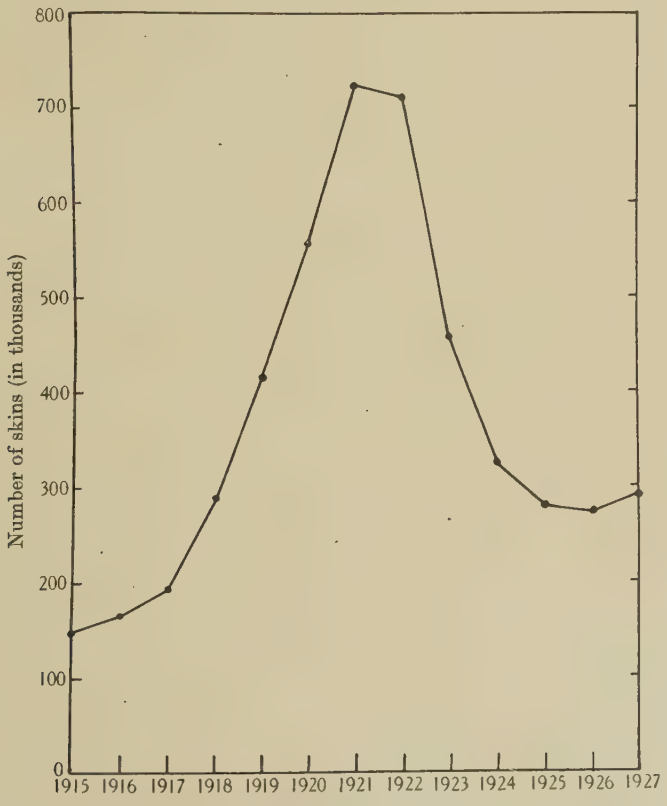


Fig. 4. Total fur returns for muskrat, Hudson's Bay Company, Outfits 1915–27, excluding those from cash-buying agencies.

If it remained irregular it was classified as 'irregular'. The 'smooth' posts practically all had peak years in 1921, 1922, or 1923, with some also in 1920.

Innis, as we have noted above, proved that abundant muskrat fur sales brought low prices, and vice versa, at any rate up to 1911. It is natural to

ask whether these price cycles themselves affected the extent of trapping in different years and might even account for part of the cycle in supplies. There

Table 5. *Prices of muskrats at London sales of the Hudson's Bay Company, in Canadian dollars and cents*

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| April | 1918 | 0.73 | | April | 1923 | 1.50 | |
| October | 1918 | 1.50 | 1.32 | October | 1923 | 1.22 | 1.38 |
| January | 1919 | 1.14 | | January | 1924 | 1.54 | |
| May | 1919 | 1.50 | | April | 1924 | 1.53 | |
| October | 1919 | 3.51 | 4.03 | October | 1924 | 1.52 | 1.40 |
| February | 1920 | 4.55 | | January | 1925 | 1.28 | |
| May | 1920 | 1.83 | | April | 1925 | 1.09 | |
| October | 1920 | 1.45 | 1.28 | October | 1925 | 1.17 | 1.22 |
| February | 1921 | 1.10 | | January | 1926 | 1.26 | |
| April | 1921 | 1.30 | | April | 1926 | 1.46 | |
| October | 1921 | 1.78 | 1.82 | October | 1926 | 1.66 | 1.75 |
| January | 1922 | 1.85 | | February | 1927 | 1.84 | |
| May | 1922 | 1.74 | | May | 1927 | 1.88 | |
| October | 1922 | 1.80 | 1.62 | October | 1927 | 2.03 | 1.97 |
| January | 1923 | 1.44 | | January | 1928 | 1.91 | |
| | | | | April | 1928 | 1.34 | |

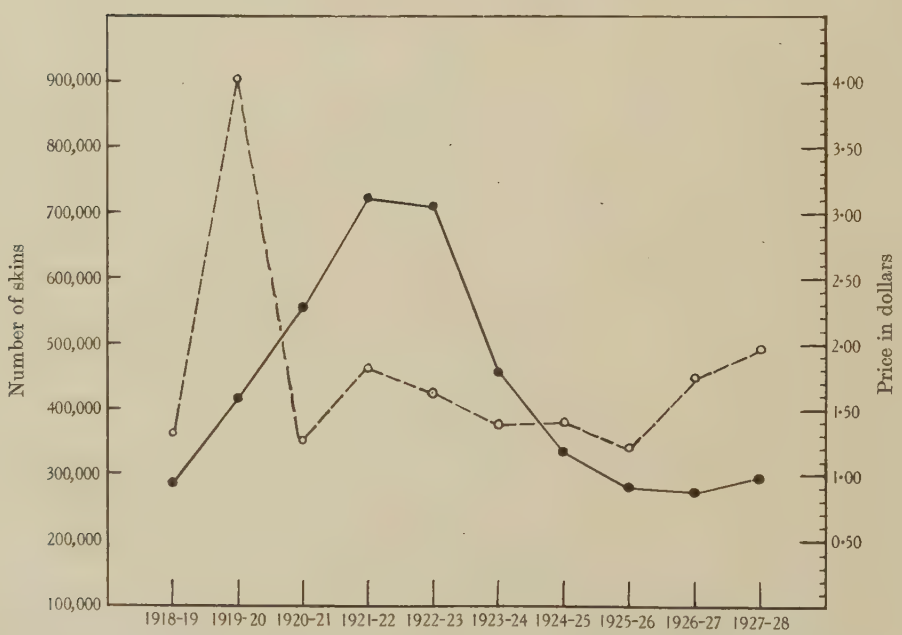


**Fig. 5. Hudson's Bay Company, total muskrat fur returns as in Fig. 4 (continuous line), and prices (dotted line), Outfits 1918–27.**

are three lines of evidence on this point. First, we know that, generally speaking, in the nineteenth century the trapper caught as much fur as he could, and that the price tariffs in the later part of the century remained

constant over long periods, irrespective of the London auction prices, knowledge of which could not reach the trappers (who were mainly natives). Secondly, we have made a special study of the MacKenzie River District archives for the nineteenth century, which prove beyond any reasonable doubt that these general conclusions applied to that region, where the ten-year muskrat cycle is well marked (Fig. 2). Thirdly, the effect of prices on the inducement to trapping activity must be much higher nowadays, with good communications and an alert white trapper population, than it was then. But the sudden price changes of the post-war boom and slump in 1919–22 do not seem to have affected the normal rise of the cycle in muskrat supplies (see Tables 4 and 5 and Fig. 5). We therefore conclude that the cycle is a real oscillation in numbers, controlling supplies. But, at the same time, it is realized that the curve for supplies is very unlikely to be a direct index of the population changes, since the trapping return per man will vary with the density of the animals trapped, to mention only one factor. But the cycle is evidently strongly enough developed to dominate the main trends of supplies, in spite of these interfering factors. This conclusion is confirmed by the reports from posts in § 7.

### 6. DOMINION FUR RECORDS, 1919–38

The Dominion Bureau of Statistics in Ottawa has published statements of furs for the whole of Canada and for separate provinces, from 1919 to 1938. (It is thought possible that these records were less complete and reliable in the first few years than later on.) The season used is July to June, instead of June to May as with the Hudson's Bay Company, but these may be taken as equivalent for the present purpose. The years are therefore rendered by us like this: 1928 = season July, 1928–June, 1929 = approximately Outfit 1928.

The figures are given in Table 6, Table 8, col. 7, and Fig. 6, the separate figures for Prince Edward Island being omitted, and New Brunswick and Nova Scotia being combined. The three Middle West provinces (Manitoba, Saskatchewan and Alberta) are also combined with Northwest Territories in a separate column, to provide some comparison with the old Northern Department of the Hudson's Bay Company. The curve for the whole of Canada shows a pronounced fluctuation, with a great peak in 1922, a minimum in 1926, followed by rise to another but smaller peak in 1928, a partial drop in 1929, and then recovery to a flat peak in 1930–3, and fall to minimum in 1936, with recovery beginning once more up to 1938, the latest figure.

The peak in 1928 is accounted for by the furs from Saskatchewan, Alberta and Northwest Territories, and it will be shown in § 8 that there was abnormal cash-buying in the southern part of the first two provinces that accounts for much of this secondary peak. The period between the two main peaks is ten years, but the second one really covered four years, as the difference between

Table 6. *Analysis of Dominion Bureau of Statistics records for muskrat production* ('1919' *means* '*season* 1919–20', *etc.*)

| Year | Canada | Nova Scotia +New Brunswick | Quebec | Ontario | Manitoba | Saskatchewan | Alberta | N.W.T. | Middle West Provinces +N.W.T. | Yukon | British Columbia |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1919 | 2,377,424 | 54,005 | 316,184 | 505,295 | 518,288 | 475,212 | 298,783 | 115,912 | 1,408,195 | 44,806 | 38,046 |
| 1920 | 2,015,481 | 44,816 | 206,987 | 462,136 | 396,180 | 246,745 | 413,612 | 156,620 | 1,213,157 | 12,765 | 72,850 |
| 1921 | 3,060,526 | 40,504 | 190,258 | 616,890 | 511,529 | 685,163 | 573,431 | 213,486 | 1,983,609 | 59,491 | 167,028 |
| 1922 | 3,846,161 | 37,602 | 192,047 | 515,386 | 602,100 | 1,352,870 | 735,653 | 219,800 | 2,910,423 | 36,960 | 152,691 |
| 1923 | 2,985,395 | 45,028 | 178,262 | 638,899 | 554,716 | 1,006,863 | 331,144 | 108,632 | 2,001,355 | 34,904 | 85,670 |
| 1924 | 2,515,142 | 49,849 | 164,645 | 534,739 | 444,386 | 856,829 | 271,633 | 79,034 | 1,651,882 | 20,929 | 92,214 |
| 1925 | 1,953,545 | 36,575 | 109,735 | 387,022 | 446,663 | 483,858 | 310,714 | 106,332 | 1,347,567 | 18,067 | 54,314 |
| 1926 | 1,774,954 | 31,296 | 128,713 | 469,947 | 226,841 | 389,436 | 306,499 | 124,879 | 1,047,655 | 12,382 | 83,954 |
| 1927 | 1,963,118 | 29,475 | 92,055 | 514,376 | 214,249 | 533,524 | 300,015 | 165,912 | 1,213,700 | 46,315 | 65,859 |
| 1928 | 2,785,994 | 45,296 | 150,345 | 714,019 | 236,895 | 775,270 | 537,556 | 248 081 | 1,797,802 | 19,284 | 56,922 |
| 1929 | 2,109,232 | 55,142 | 145,671 | 643,999 | 252,657 | 432,893 | 274,811 | 145,858 | 1,106,219 | 92,953 | 64,022 |
| 1930 | 2,639,086 | 71,059 | 223,246 | 723,325 | 302,232 | 401,335 | 510,036 | 269,839 | 1,483,442 | 52,158 | 84,500 |
| 1931 | 2,632,984 | 47,767 | 190,867 | 640,390 | 442,960 | 361,523 | 512,977 | 287,149 | 1,604,609 | 41,545 | 106,920 |
| 1932 | 2,731,490 | 38,415 | 172,343 | 637,348 | 421,799 | 590,453 | 555,391 | 184,027 | 1,751,670 | 34,902 | 94,477 |
| 1933 | 2,538,565 | 35,930 | 165,773 | 522,493 | 385,066 | 686,062 | 544,808 | 118,537 | 1,734,473 | 30,386 | 48,851 |
| 1934 | 1,983,747 | 53,810 | 145,015 | 444,728 | 321,828 | 378,285 | 404,428 | 101,044 | 1,205,585 | 24,471 | 107,536 |
| 1935 | 1,630,231 | 47,945 | 115,496 | 359,294 | 255,747 | 197,979 | 397,029 | 136,257 | 987,012 | 25,337 | 93,796 |
| 1936 | 1,607,897 | 64,916 | 116,912 | 361,083 | 334,516 | 98,768 | 274,640 | 220,025 | 927,949 | 34,419 | 101,041 |
| 1937 | 1,748,239 | 68,686 | 128,245 | 471,203 | 291,489 | 46,699 | 199,285 | 422,399 | 959,872 | 48,445 | 70,589 |
| 1938 | 2,295,550 | 73,687 | 188,278 | 687,711 | 319,968 | 211,740 | 237,224 | 429,275 | 1,198,207 | 62,385 | 83,589 |

1932 and the other three years is negligible. Whereas the peaks in the three Middle West provinces came simultaneously in 1922, they were in three different years in 1931–3. This difference in geographical incidence (very characteristic of all regional analysis of the ten-year cycle for any fur) may be illustrated thus:

1922 Middle West, Northwest Territories
1923 Ontario
1930 Ontario
1931 Manitoba, Northwest Territories
1932 Alberta
1933 Saskatchewan

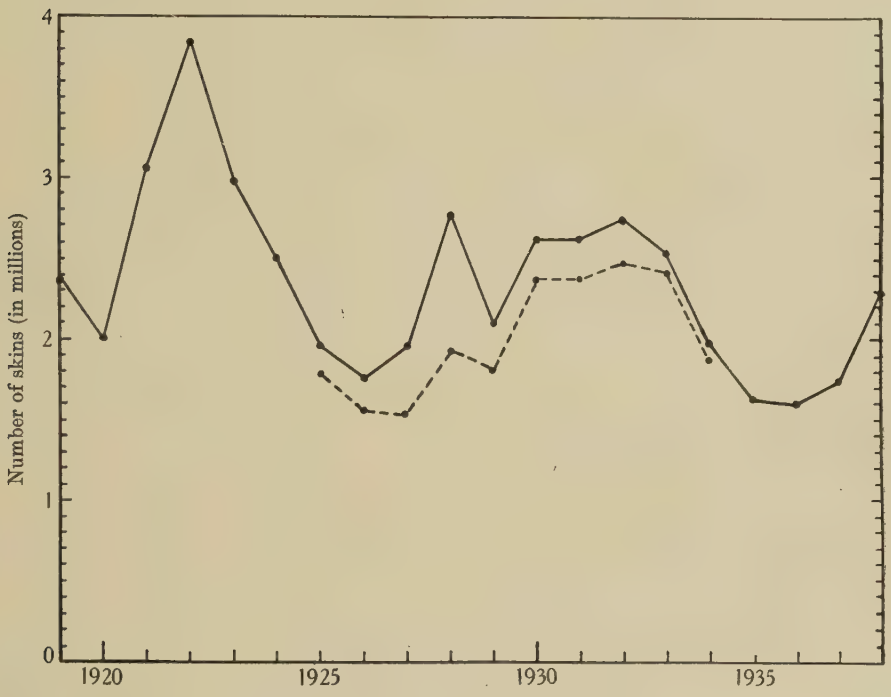


Fig. 6. Fur returns of muskrat, all Canada, 1919–39 (Dominion Bureau of Statistics). Lower broken line is the Dominion totals minus cash-bought Hudson's Bay Company skins from the southern parts of the three Middle West Provinces.

The totals recorded both for Canada and the Middle West plus Northwest Territories are on the average much bigger than any reached by the Hudson's Bay Company total sales in early days or the Northern Department fur returns respectively. This indicates that although the Company inevitably lost trade when competition grew up, there has also been a greater total exploitation of muskrat fur resources, which is not surprising in view of the huge price increases that occurred in the present century.

### 7. Annual reports from Hudson's Bay Company posts, 1925–39

In 1925 Mr Charles V. Sale, then Governor of the Hudson's Bay Company, with the advice of Mr (now Sir) George Binney and of Elton, started an annual questionnaire to the Company's fur-trade posts in order to get opinions on the changes of abundance of some cyclical species. These reports have been of great value, since they are not simply based upon the annual fur catch, but represent an attempt on the part of post managers to ascertain by personal observation and by inquiry among white and native trappers and other field men the real position of animal populations in the region covered by each post's operations.

Table 7. *Summarized reports from Hudson's Bay Company posts (mainly in northern forest belt, Arctic posts omitted) for Outfits* 1924–39 *(no record for* 1931), *giving comparisons of abundance with previous year*

| | Increase | | No change | | Decrease | |
|---|---|---|---|---|---|---|
| Year | No. | % | No. | % | No. | % |
| 1924/25 | 1 | 6 | 0 | 0 | 16 | 94 |
| 1925/26 | 4 | 19 | 0 | 0 | 17 | 81 |
| 1926/27 | 5 | 22 | 1 | 4 | 17 | 74 |
| 1927/28 | 6 | 25 | 2 | 8 | 16 | 67 |
| 1928/29 | 18 | 42 | 3 | 7 | 22 | 51 |
| 1929/30 | 21 | 39 | 8 | 15 | 25 | 46 |
| 1930/31 | 43 | 77 | 5 | 9 | 8 | 14 |
| 1932/33 | 58 | 47 | 9 | 7 | 56 | 46 |
| 1933/34 | 33 | 30 | 10 | 9 | 66 | 61 |
| 1934/35 | 19 | 17 | 5 | 4 | 90 | 79 |
| 1935/36 | 27 | 21 | 9 | 7 | 92 | 72 |
| 1936/37 | 36 | 27 | 17 | 13 | 82 | 60 |
| 1937/38 | 87 | 57 | 20 | 13 | 46 | 30 |
| 1938/39 | 93 | 66 | 26 | 18 | 21 | 16 |
| 1939/40 | 116 | 71 | 26 | 16 | 21 | 21 |

With the realization that subjective estimates of absolute numbers could have no standard meaning for comparing either different places or different years, these reports are arranged on a system of year to year comparisons: 'Was the muskrat *more abundant* or *less abundant* this Outfit than last Outfit?' Some other questions are also asked, but these are subsidiary, the main object being to get a running record from year to year. Such a record is, of course, only of much use for a fairly regular cycle such as is met with among many Canadian fur-bearers, and it needs to be made at a large number of posts in order to smooth out individual mistakes and other random errors. The results for the muskrat for a period of 15 years are given in Table 7, and on a series of maps in Figs. 7–20. The territory of each post here used as a convention—100 miles across—gives a substantially true general impression, since it is not far removed from the average covered by many posts (at any rate outside the Arctic regions, where the muskrat does not occur).

The number of posts sending in reports increased gradually up to 1930. No reports were made in 1931. From 1932 onwards practically every post was reporting, and most of these reports were in a form that could be used here. The maps up to 1928 give a smaller, random sample of posts for each year, but this reflects the main trends of the cycle. The later maps provide an almost complete network of areas covering in aggregate a great deal of the northern forest belt of Canada.

The cycle stands out clearly to the eye, and the percentage of posts reporting increase each year (i.e. the percentage of black discs) is summarized graphically in Fig. 21. It started from a low point in 1924 and rose steadily up to 1930, when it stood at 77%. By Outfit 1932 it had dropped to 47%, much of this decrease having taken place not in the breeding season of year 1931 but (as remarks in the reports prove) in the autumn, winter or spring of 1932–3. It is possible that 1932 was the peak year, but the absence of records for 1931 makes this uncertain. The drop in 1932 continued to a low point of 17% in 1934, just ten years after the previous low point of 6% in 1924. But as the records only began in that Outfit, we cannot say for certain that 1924 was the minimum year of that cycle, though it evidently was either at or very near it.

On the whole, the onset of increase is distributed in a random manner throughout the whole zone, and it is difficult to make finer analyses of geographical differences, since records of this nature (subjective opinions averaged over a large stretch of country) can only afford a rough instrument for measuring the cycle, and a breakdown of the records into smaller groups would suffer from larger random errors. But the maps strongly confirm conclusions from the fur figures that the cycle is a real one in the field; that it

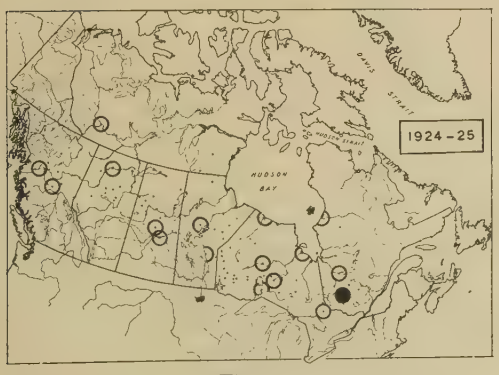


Fig. 7

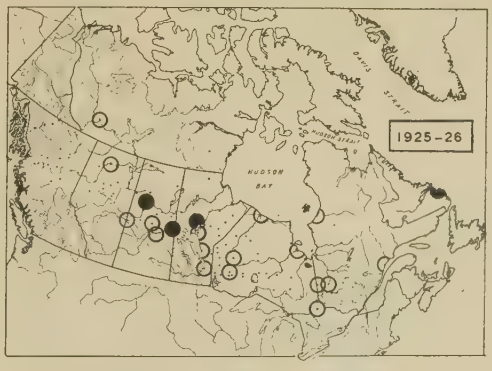


Fig. 8

Figs. 7–20. Reports from Hudson's Bay Company posts for Outfits 1924–39 (no record for 1931). The symbols represent comparisons of abundance with the previous year: solid black discs are increase; dotted discs are no change; and plain circles are decrease. Each symbol has a radius of 50 miles, except where the posts are less than 100 miles apart, in which case an equal division is made between them.

Fig. 9

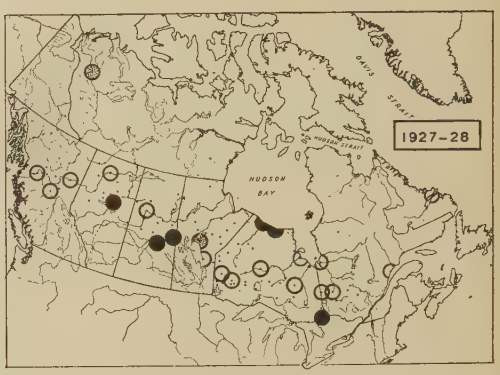


Fig. 10

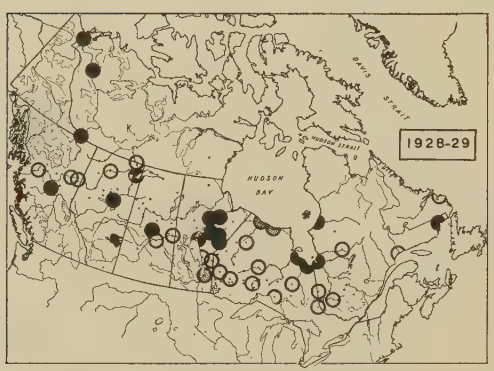


Fig. 11

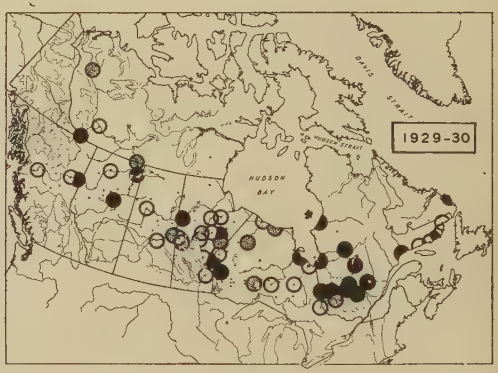


Fig. 12

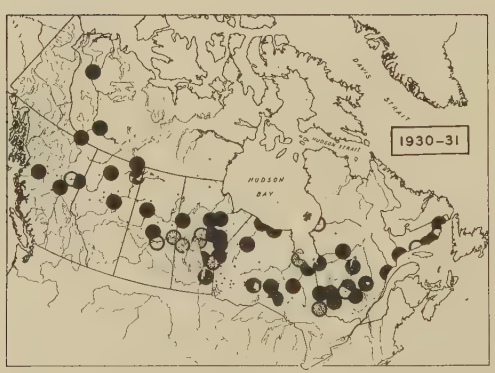


Fig. 13

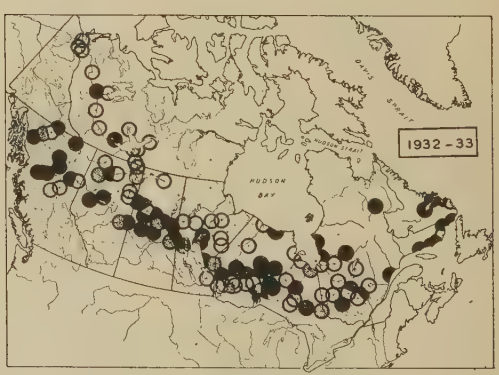


Fig. 14

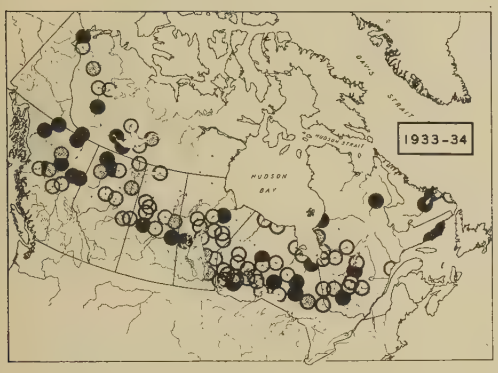


Fig. 15

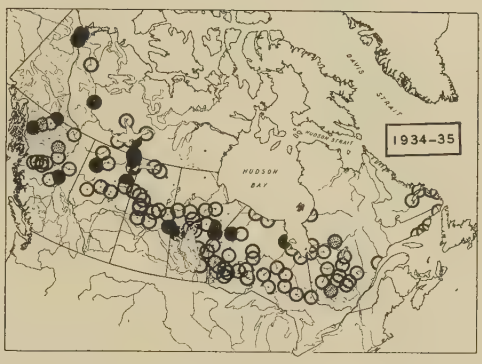


Fig. 16

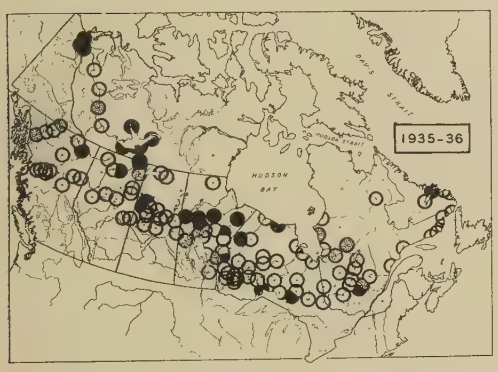


Fig. 17

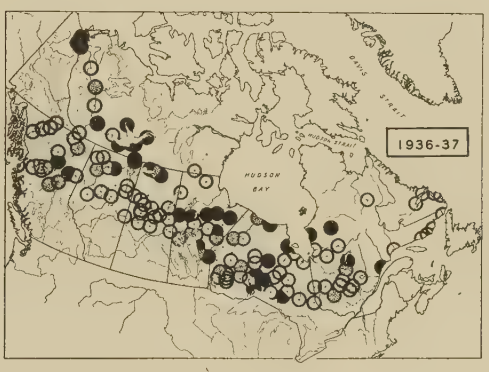


Fig. 18

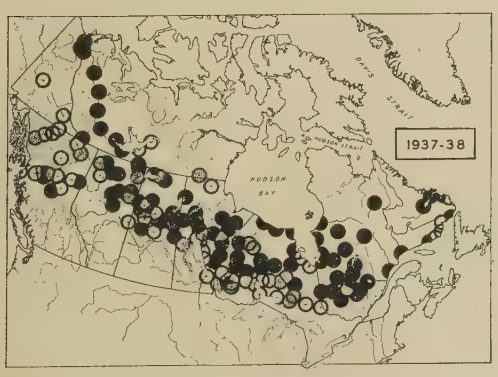


Fig. 19

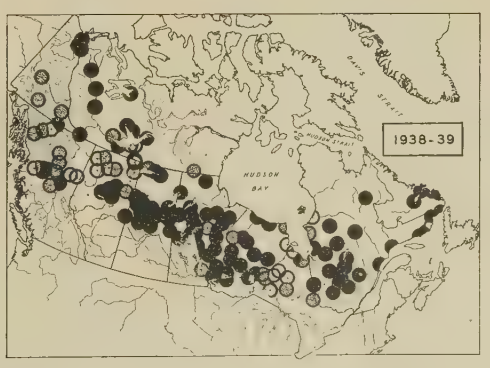


Fig. 20

operates in a roughly synchronous way over a huge belt of Canada; that it had a peak about 1932 and was in 1939 approaching another; and that the 'ten-year' cycle shown in the earlier fur returns is still acting in full force as a vital influence on muskrat supplies.

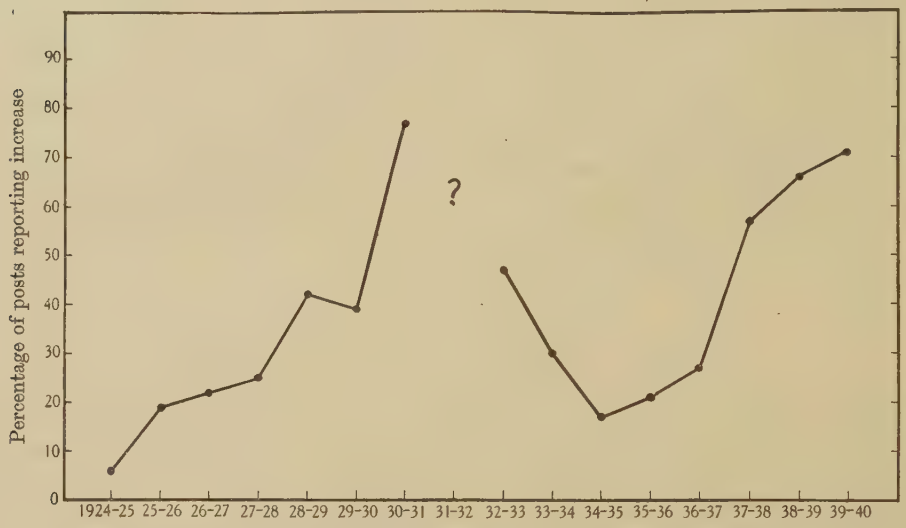


Fig. 21. Percentage of Hudson's Bay Company posts reporting muskrat increase, Outfits 1924–39 (no record for 1931).

## 8. Fluctuations in the southern part of the Middle West

We have shown that, whereas the total Dominion figures, and particularly those for Saskatchewan and Alberta, have a marked separate peak in 1928, no such anomaly appears in the total fur returns of the Hudson's Bay Company, provided that the furs from cash-buying agencies are omitted. The returns, and also the reports from posts, indicate a smooth cycle with two peaks, in 1921–2 and in 1930 or 1931, corresponding to the total Dominion fur peaks in 1922 and 1930–3. This point requires further elaboration.

In 1927–8, while the muskrat cycle was at a low point in the northern forest region, there were considerable areas of high productivity in the southern part of the Prairie Provinces. The following notes were collected by Elton during a tour across Canada made during the summer of 1928 on behalf of the Hudson's Bay Company. Mr F. Bradshaw, Game Commissioner of Saskatchewan, said that when muskrat scarcity began to be noticeable in the northern woods from about 1923 and 1924 onwards, an area in the south-east of Saskatchewan remained unaffected and was still producing muskrats in 1927. The area referred to lies mainly in the aspen park-land country known as the 'grove belt', though it also includes some places on open prairie; it is defined roughly on the west by a line between Saskatoon and Regina and on the east

by the Manitoba boundary opposite Canora down to the southern corner. The published reports of the Game Guardian (Bradshaw) record this abundance as being well marked already in 1925–6. It is interesting to find in his report for 1920–1 that: 'The fall trapping of muskrats south of township fifty-two was prohibited last season, but owing to the excessive trapping of previous years, and the dry seasons that have prevailed lately, muskrats are very scarce in the greater part of this territory....The breeding stock has been reduced to...a low ebb....' The belt south of Township 52 (which itself lies a little north of the town of Prince Albert) falls within the prairie and grove belts, and includes the smaller block mentioned by Mr Bradshaw as having continued abundance after 1924 and up to 1927.

Table 8. *Muskrat fur returns from cash-buying agencies, Hudson's Bay Company*, 1915–34

| | Southern Middle West agencies | | | | | Dominion total less southern Middle West agencies |
|---|---|---|---|---|---|---|
| | Winnipeg | Prince Albert | Regina | Edmonton | Total | |
| 1915 | — | 12,708 | — | — | 12,708 | — |
| 1916 | — | 1,146 | — | — | 1,146 | — |
| 1917 | — | 1,520 | — | 207 | 1,727 | — |
| 1918 | — | 95 | — | 62 | 157 | — |
| 1919 | — | 2,243 | — | 536 | 2,779 | — |
| 1920 | 12,762 | 3,467 | — | 30,790 | 47,019 | — |
| 1921 | — | 11,898 | — | 37,801 | 49,699 | — |
| 1922 | 40,181 | 26,308 | — | 58,008 | 124,497 | — |
| 1923 | 46,724 | 18,898 | — | 56,548 | 122,170 | — |
| 1924 | 60,663 | 453 | — | 41,536 | 103,052 | — |
| 1925 | 45,756 | 15,541 | — | 45,062 | 106,359 | 1,847,186 |
| 1926 | 60,731 | 11,109 | — | 22,402 | 194,543 | 1,580,411 |
| 1927 | 183,471 | 56,546 | 100,300 | 86,326 | 426,643 | 1,536,475 |
| 1928 | 258 866 | 37,603 | 385,551 | 186,391 | 868,411 | 1,917,583 |
| 1929 | 69,697 | 23,310 | 145,744 | 79,434 | 318,185 | 1,791,047 |
| 1930 | 51,950 | 28,185 | 28,720 | 173,716 | 282,571 | 2,356,515 |
| 1931 | 73,797 | 26,909 | 7,652 | 169,827 | 278,185 | 2,354,799 |
| 1932 | 46,542 | 39,802 | 10,505 | 157,990 | 254,839 | 2,476,641 |
| 1933 | 23,371 | 42,053 | 8,742 | 114,974 | 189,140 | 2,349,425 |
| 1934 | 18,349 | 21,523 | 5,239 | 55,185 | 100,296 | 1,883,451 |

These records prove that there was muskrat scarcity in this southern area just at the time when the northern populations were approaching a peak, and muskrat abundance there for several years after the latter had crashed to their periodic low numbers. The line between these two different regimes seems to have followed the grove belt. A similar southern abundance was reported from Alberta by Mr T. E. Randall, an experienced field observer, who reported that muskrats were extremely numerous in southern Alberta in 1928, all the sloughs swarming with them, and that the water was not particularly low.

This inverse abundance of the southern Middle West seems to be reflected in the cash-buying activities of the Hudson's Bay Company. The figures from 1915 to 1934 are given in Table 8. The extra peak in the total Dominion furs almost, though not entirely, disappears, if the cash-bought Hudson's Bay

Company furs from their southern Middle West agencies are subtracted (Fig. 6). It was shown in § 5 that this peak is completely absent from the Company's fur-post totals, which do not include any cash-bought muskrats. We are left with the suggestion that the great numbers of skins collected in the Middle West cash-buying centres during the low period of the northern cycle were mainly obtained from the settled prairie and grove-belt parts, on account of the inverse cycle of abundance that these underwent. This conclusion is supported by a statement from the Regina office of the Company in 1928, that the main source of their furs at that time was in much the same area of Saskatchewan as that defined by Mr Bradshaw, and especially in the south-eastern part of it. It is known that other traders besides the Hudson's Bay Company were obtaining furs from these regions at the same time.

The southern story can be traced in later years also by indirect means and through a few game warden's notes. By 1930 there had developed a very serious and in places catastrophic drought, in the prairie provinces of both Canada and the United States, which not only ruined many farmers but also grievously affected the breeding populations of waterfowl on bodies of water over the whole of that region. As a result we have some reliable records which tell us by implication at the same time the fate of the muskrats. In February 1930, Lloyd, Superintendent of Wild Life of the National Parks Bureau in Ottawa, wrote: 'All fall I have been travelling through the duck belt of Canada. Ponds, prairie sloughs, shallow lakes are very largely dry in the Western Provinces. If not completely so, they are fringed with dry mud, or often reduced to a remnant of alkali-fringed water. Mr Fred Bradshaw, Director of the Provincial Museum of Saskatchewan, said that water shrinkage of this kind in that Province amounted to ninety per cent.' The annual report of the Hudson's Bay Company's post Fort à la Corne, which is situated just on the border of the grove belt and the northern forest of Saskatchewan, stated for Outfit 1930: 'Ducks and muskrats scarce, due to dry season.'

It is reasonable to suppose that this prolonged drought must have reduced the muskrat populations as well as those of the ducks, and a fall is shown in the Company's southern Middle West cash-bought skins (Table 8). By 1935 Lloyd was able to report that the conditions of waterfowl in these regions had shown a temporary revival after six years of drought: 'In that portion of the Canadian duck-nesting area, situated in the southern part of the Prairie Provinces, Alberta, Saskatchewan and Manitoba, water conditions were much improved over those of the past few years.' (His rainfall chart shows 1929 as the lowest year, but in the (for ducks) critical season up to the end of July each year, it remained comparatively low in 1929, 1930, 1931, 1933 and 1934, with somewhat higher levels in 1932 and 1935.) 'In the wooded area lying to the north of the prairie duck breeding grounds in Alberta and Saskatchewan, water conditions continued approximately normal during 1935. That area did not suffer to any great extent from the last drought' (Lloyd, 1936).

But in 1936 there was again a spectacular drought during which water and ducks vanished from wide stretches of the prairie provinces: 'The Chief Migratory Bird Officer for the district, who made an extensive inspection trip through southern parts of Manitoba, Saskatchewan and Alberta last summer, reported that he drove for hundreds of miles without seeing a single natural pond or pool of surface water, or a duck of any kind and that these were the conditions he found in the midst of the old hereditary breeding grounds where water fowl once bred in abundance' (Lloyd, 1937). By 1939, Lloyd reported that 'the drought cycle appears to be broken at last' (1940).

The reports of the Game Warden of Saskatchewan for some of these years contain references to the effect of this drought upon muskrat fur production (the years of reference cover twelve months ending 30 April—approximately equivalent to the Hudson's Bay Company Outfit).

1935–6. 'A substantial reduction is shown in the number of wild fur animal pelts marketed...possibly accounted for, to some extent, by the almost complete disappearance of the muskrat from the large area within the agricultural belt affected by drought, as well as to cycles affecting wild fur animal life.'

1937–8. 'This decrease of 51% in the total value of all furs produced in the Province may be attributed to the low point in the cycle and drought conditions, the drop in market values during the earlier part of the season, and finally, the closing of the season on muskrat.'

1938–9. 'With more normal precipitation and the policy of closed season south of the Churchill River during the trapping season of 1937–8, more of...the muskrat were noted in their former haunts. Open season was declared in the spring of 1939, resulting in a large increase in the number of pelts taken in the area lying north of Township 53, the area in which it was considered the Muskrat was plentiful.'

Evidently muskrats were still scarce at this time in the country south of Township 53, and we feel justified in assuming from all this converging evidence that from at least 1930 onwards these southern populations did not again contribute substantially to the total fur production of muskrat furs in Saskatchewan and Alberta, and therefore are unlikely to be causing any abnormalities in the curve of increase for the present cycle. This conclusion is confirmed by examination of the Hudson's Bay Company cash-bought skins for the Middle West, up to 1940 (partly listed in Table 8).

Although the inverse movement up and down of the northern and southern muskrat populations between 1915 and 1935 is apparently a fact, and a striking one, we are not scientifically justified in concluding from it alone either that there has been a regular ten-year cycle in prairie and grove-belt aquatic animals brought about by rainfall cycles, or that the northern ten-year cycle in the forest zone is controlled by similar cycles in water-level. Lewis & Dowding (1926) found some evidence of long-term cycles in rainfall from measurements of the annual rings of growth in trees growing in muskegs in the poplar belt of Alberta. These indicate a great peak of growth around 1835, followed by decrease until the end of the century, when growth again increased up to higher levels again in 1925. If we can safely refer these changes to

long-term rainfall variations, it would seem from them and from the other facts already described that the second cycle of increase reached its peak by or before 1929, after which the intense droughts began to be experienced. In 1921 Soper recorded that the continued drying up of the lakes and ponds around Islay, lying in the same region of Alberta, had considerably reduced the muskrat populations: 'It is estimated that between one and two thousand muskrats inhabited the dried-up lake west of Islay in pre-settlement days' (p. 108). It seems probable that the behaviour of the southern cycle in relation to the shorter northern one may have been a coincidence. This conclusion is borne out by the extreme severity of the recent drought period, and by the failure of the southern muskrats to show any great recovery in 1937–8.

As regards the causes of the ten-year cycle in the muskrat populations of the northern forest zone, many interesting hints and theories could be set down, but there is still no evidence good enough to establish scientifically a recurrent influence of water-level changes which would explain the cycle. Seton, for instance, mentions (1912, p. 109) that: 'The muskrat's variation probably has relation chiefly to the amount of water, which, as is well known, is cyclic in the north-west.' There seems to be a fairly widespread belief among fur traders and naturalists that the periodic crash in numbers is brought about chiefly by the muskrats freezing to death when low water, with or without an unusually severe winter, occurs in the winter.

We have found numerous instances mentioned in the Hudson's Bay Company's annual reports from posts, of muskrat mortality, usually though not always associated with decrease in numbers in the region of the post. Three main causes are given: freezing to death (from severity of the winter, lack of snow, thick ice, etc.), drowning (from high water in autumn, or snow-melting floods in spring, etc.), and epidemic (usually without any definite symptoms described). No doubt these three categories are not always clear-cut, since, for instance, a muskrat found frozen into a lake in the spring might have died from illness, while some of the epidemics might have been due to climatic extremes and wrongly attributed to disease. The winter of 1930–1 was reported to be extremely mild, while that of 1932–3 was reported to be exceptionally severe over large parts of Canada, in some places with very little snow. There were virtually no records of mortality in 1930–1, but in 1932–3 about a third of the 123 posts giving muskrat data reported mortality, and about three-quarters of these records were of muskrats being found frozen to death. That winter marked the first or second year of the crash (the doubt being due to the absence of records for 1931–2). The winter of 1933–4 was also rather severe, though less generally so, and mortality was again reported from about a third of the 109 posts concerned, but only about a third of the mortality records were of freezing.

We do not wish to place too much weight on these records, but they at any rate suggest that climatic factors may have played a dominant part in

the crash during this particular cycle. If the same set of circumstances appears at and after the next peak, for which more complete data will be available, we shall consider that a strong case has been made out for the climatic control of the muskrat cycle, and therefore for the association of climatic recurrences with the ten-year cycle as a whole. There is great need for exact measurements of water levels, snow depths and temperature in relation to sample field populations of muskrats, and opportunities for these should be available in the new muskrat conservation projects, about which something may now be said, as their future depends to some extent on the truth or otherwise of the theories discussed in the present paper.

## 9. Muskrat reserves

Intensive muskrat farms, along the lines of fox and mink farms, have been tried to some extent, and some breeders have undertaken to keep muskrats in ordinary pens without water. But the total number of skins sold from fur farms in 1938 was only 4921, a figure which could not have affected any conclusion about the raw fur production of Canada. In previous years the numbers were less than this. But at the same time a much more important method of encouraging muskrat production was being developed, by taking large tracts of marsh-land and lake and river, and attempting to manage the populations under semi-natural conditions. The chief measure taken has been control of the water-level, by building fairly elaborate engineering works such as dams and sluices, the idea being to prevent the recurrent lowering of water which had caused such destruction in some winters, and thereby to maintain high and approximately constant numbers. Although these projects have all been started in a purely empirical manner, the essential idea underlying them is to iron out the effects of cyclical fluctuations in the population, and at the same time build up the numbers to higher levels than can be achieved under uncontrolled conditions. A general account of the development of these projects in Manitoba since 1930 has been published by Denmark (1937), and the beginning of field ecological studies on muskrat food conditions by Butler (1940). It will be of intense interest to observe whether the next crash in natural muskrat populations after their peak, will be prevented on these controlled reserves, or whether some factor or factors other than water-level is involved. The reserves offer a sort of natural experiment whose scale is very large, since individual reserves may run into hundreds of thousands of acres, although the cropping from them cannot have greatly influenced the total production of Canada until very recently.

## 10. Conclusions about the muskrat cycle

Each line of evidence contains certain sources of error when it is used as an index of changes in the muskrat population, and to these we may partly attribute the slight amount of disagreement between the dates for peak and

minimum in each cycle. These years are summarized in Table 9, and they agree sufficiently closely to show the real existence of a cycle in Canadian muskrat populations of about ten years in length and of very wide geographical extent in the forest belt of Canada.

Table 9. *Summary of muskrat cycle*

Peak years in heavy type. Minimum years in ordinary type.
Peak due to southern increase, in brackets.

| | H.B. Co. Fur Returns | | | | | |
|---|---|---|---|---|---|---|
| H.B. Co. Total Fur Sales | N. Dept. | MacKenzie R. District | Total, minus cash-buying agencies | H.B. Co. Reports from Posts | Dominion Fur Records (Canada) | Range of dates (omitting MacKenzie R. District) |
| — | 1849 | — | — | — | — | 1849 |
| — | **1852** | — | — | — | — | **1852** |
| — | 1858 | — | — | — | — | 1858 |
| — | **1862** | — | — | — | — | **1862** |
| 1868 | 1866 | — | — | — | — | 1866–8 |
| **1871** | **1872** | **1870** | — | — | — | **1870–2** |
| 1875 | 1876 | — | — | — | — | 1875–6 |
| **1880–2** | **1880** | **1878–9** | — | — | — | **1880–2** |
| 1887 | 1887 | — | — | — | — | 1887 |
| **1891** | *c.* **1890**? | **1889** | — | — | — | **1890–1** |
| **1894** | — | — | — | — | — | **1894** |
| 1895 | *c.* 1898? | — | — | — | — | 1895–8 |
| **1900** | **1901** | **1899–1900** | — | — | — | **1900–1** |
| 1906 | 1906 | — | — | — | — | 1906 |
| — | *c.* **1912** | **1909** | — | — | — | **1912** |
| — | — | — | *c.* 1915 | — | — | *c.* 1915 |
| — | — | **1921** | **1921–2** | — | **1922** | **1921–2** |
| | — | — | 1925–6 | *c.* 1924 | 1926 | 1924–6 |
| | — | — | — | — | (**1928**) | (**1928**) |
| — | — | — | — | **1930 or 1931** | **1930–3** | **1930–3** |
| — | — | — | — | 1934 | 1936 | 1934–6 |

Apart from the large numbers obtained about 1928, which are accounted for by the southern populations in the Middle West (§ 8), the only major discrepancy is the sales peak in 1894, the source of which we do not know, as Northern Department fur returns are lacking for the years 1892–6. If the 1894 peak be omitted, we are left with a series of peak years recurring at the same sort of interval as those of the lynx and snowshoe rabbit: nine peaks or eight periods in about 80 years. These figures leave little doubt as to the presence of a common factor affecting the population cycles of both terrestrial and aquatic animals in the Canadian forest zone. Confirmation is given by the remarkable analysis of the salmon catches in the Restigouche River, New Brunswick, done by Phelps & Belding (1931) who found an undoubted cycle in numbers with peak years in 1885–6, 1895, 1905–6, 1917, 1924–5, the controlling source of which they believed could be shown by study of salmon age-class distribution, to be in the marine or estuarine life of the fish, not in the river itself. There is here a hint of a still wider nexus of conditions behind the ten-year wild-life cycle, through oceanography and climate combined. It

is important that the muskrat peak precedes by a year or two the main snowshoe rabbit and lynx peaks. This point will be taken up in our forthcoming study of the lynx cycle.

## 11. SUMMARY

1. Analysis of fur sales and fur returns of the muskrat (*Ondatra zibethica*) in the nineteenth and twentieth centuries, together with a questionnaire enquiry to fur posts in Canada, shows that there has been, since about 1850 at any rate, a strongly marked cycle in numbers of muskrats with an average period of recurrence of about ten years.

2. An anomaly about 1928 can be accounted for by the effects on the figures of muskrat abundance in the southern part of the Middle West of Canada, resulting from a long-term fluctuation in rainfall.

3. The ten-year cycle in muskrats has a very wide geographical range, right across Canada, and it runs parallel with the similar cycle in numbers of snowshoe rabbits (*Lepus americanus*), and various terrestrial fur-bearing animals, game birds and raptorial birds.

4. The presence of parallel cycles in aquatic and terrestrial species in the same region affords strong evidence for the existence of some climatic factor controlling these different population rhythms.

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# THE HABITAT DISTRIBUTION OF THE GREY SQUIRREL (*SCIURUS CAROLINENSIS*) IN SAVERNAKE FOREST

By M. K. COLQUHOUN

## 1. Introduction

During a preliminary survey of Savernake Forest, Wiltshire, sample counts were recorded of the number of grey squirrels (*Sciurus carolinensis* Gmelin) observed for a period of some six months. The method used was to record the number of squirrels seen per hour while walking through the Forest, the usual observing speed being about 1 mile per hour. The grey squirrels of the Forest are regularly shot, but in a keeper's opinion are still increasing; the same keeper had not seen a red squirrel (*Sciurus vulgaris*) for six years. Since the Forestry Commission took over Savernake it was apparently intended to keep down the squirrels more energetically, but further action may have been postponed because of the war.

The Forest has been described in a previous paper (2), which also notes changes which may be expected to follow the work of the Commission. It consists of ancient oaks (*Quercus robur*), with varying sparse growth of hawthorn (*Crataegus oxyacantha*) scrub. There is seldom a closed canopy, but some of the drives run through dense avenues of beech (*Fagus sylvatica*), which also form clumps on the high ground.

## 2. Sample counts

All the counting was done in the mornings. The monthly totals of the counts recorded in the Forest were as follows:

| 1938–9 | Squirrels counted | No. of hours | Squirrels per hour | Percentage observed in trees | Percentage observed on ground |
|---|---|---|---|---|---|
| October | 5 | 3·00 | 1·7 | 40 | 60 |
| November | 27 | 5·50 | 4·9 | 15 | 85 |
| January | 16 | 2·75 | 6·0 | 56 | 44 |
| February | 20 | 11·03 | 1·8 | 36 | 64 |
| March | 22 | 10·00 | 2·2 | 18 | 82 |
| April | 31 | 12·50 | 2·5 | 20 | 80 |
| May | 11 | 9·00 | 1·2 | 27 | 73 |
| June | 84 | 25·83 | 3·3 | 12 | 88 |

The squirrel per hour index for the whole period is 2·7; for the first four months it is 3·0, and for the last four, 2·6. The opening of the foliage renders a squirrel almost completely inconspicuous in most trees, but there is an

increase in the population when the young become active, and it is likely that these two factors counterbalance each other to a certain extent. The rise in the index for June, when the young are about, occurs when the trees are fully in leaf; the May figure suggests that the young were not then active enough to counteract the increase in foliage. The habits of the squirrels themselves also affect their conspicuousness. In autumn they spendmuch time on the ground, searching for acorns and beech mast, and are therefore easily seen; although if an observer moves quietly the grey squirrel in winter is almost as conspicuous in a tree, particularly on the smooth bark of a beech, as it is on the ground. The high indices for November and January may partly be due to this ground feeding, but may also be the results of more intense activity in fine weather during the short winter days. Because normal weather (absence of extremes) was selected for the actual counts, no day-to-day variation in squirrel activity was noticed, but field observations showed that squirrels, perhaps even more than birds, are less active in warm weather, particularly towards noon.

The monthly percentages showing where the squirrels were first observed are founded on too few counts to give more than a rough idea of variations in squirrel conspicuousness or behaviour; however, 73 % of all the squirrels seen up to the end of April occurred on the ground, while the figure for May and June together is 86 %, confirming that when the trees are in leaf very few squirrels are seen which are not on the ground.

Because of these variations in conspicuousness, summer and winter counts should not be used indiscriminately for comparing relative populations. Winter is undoubtedly the ideal season for sampling a population of animals inhabiting deciduous trees, and it is probably advisable to confine the counting to either early, mid or late winter, if it is intended to compare counts in different habitats or woods.

### 3. Observing speed

For comparison, counting was done at two different observing speeds over the same course, which was 2·31 miles long. The course was covered five times at each speed, in alternate directions, the five walks being completed within a period not longer than a fortnight; this was done in mid-February, and repeated in early June. Counting was confined to the mornings, days of abnormal weather being avoided. From the following counts only those at the slower walking speed have been included in the previous table:

| 1939 | Observing speed m.p.h. | No. of hours | Squirrels counted | No. per hour | No. per mile |
|---|---|---|---|---|---|
| February | 1·05 | 11·03 | 20 | 1·8 | 1·7 |
| | 2·46 | 4·70 | 8 | 1·7 | 0·7 |
| June | 1·09 | 10·67 | 41 | 3·8 | 3·6 |
| | 2·27 | 5·08 | 29 | 5·7 | 2·5 |

The slow-fast ratios of the different indices are very similar to those found for birds (**1**), as will be seen from the following comparison:

| | | Ratio between observing speeds | Ratio between nos. per hour | Ratio between nos. per mile |
|---|---|---|---|---|
| Squirrels: | February | 2·3 | 0·9 | 0·4 |
| | June | 2·1 | 1·5 | 0·7 |
| Birds: | February | 2·3 | 1·7 | 0·7 |
| | June | 2·1 | 1·7 | 0·8 |

(In February, the total number of squirrels recorded was very low.) As would be expected, the number of squirrels or birds seen per hour is greater when an observer walks more quickly, but the increase is not proportional to the increase in speed—as it should be theoretically, in an evenly distributed population with unvarying conspicuousness. But an increase in the observer's speed decreases the visual and auditory conspicuousness of all animals, simply because he has less time to observe; it was for this reason that the slower walking speed (about 1 mile per hour) was recommended for sample counts of birds.

### 4. Habitat distribution

Counts in oak and beech were recorded separately, and being undertaken concurrently, may be usefully compared:

| | Squirrels counted | No. of hours | Squirrels per hour | Seen on or under beech | Seen on ground under beech |
|---|---|---|---|---|---|
| Oak dominant (sparse hawthorn) | 193 | 66·66 | 2·9 | 88 (46%) | 79 (90%) |
| Beech dominant | 32 | 7·00 | 4·6 | 28 (88%) | 24 (68%) |

The February counts have been omitted because the records were incomplete; when they are included the squirrel per hour index is 2·7 instead of 2·9. Any sectional walk through the oak parts of the Forest is liable to cut across a beech avenue, or to encounter occasional beeches, but the number of beeches so encountered would be under 5% of the total trees; yet it will be seen that 46% of the squirrels were observed on or under beeches. Actually, this underestimates the preference for beech, since many squirrels were recorded under oaks when a beech tree was in the neighbourhood, and not infrequently they would scamper across to the beech when disturbed. But the preference was most obvious during the repeated walks over the set course; every squirrel except one pair had their home in a beech, although they were sometimes recorded as feeding under oaks. The percentage seen on or under beeches (46%) was exactly the same summer and winter. The percentage of squirrels seen on the ground under beeches is of those in the previous column. The lower percentage recorded on the ground among pure stands of beech may be partly due to the greater auditory conspicuousness of squirrels in this tree.

The following counts in pure beech may also be compared:

| | No. of hours | Squirrels per hour | Jackdaws per hour |
|---|---|---|---|
| 'Grand Avenue' | 2 | 3·5 | 31·0 |
| 'Three Oak Hill Drive' | 2 | 8·5 | 2·0 |

These were recorded between the end of April and beginning of June, at a walking speed of exactly 1 mile per hour, and seem to suggest an inverse relationship (competition?) between the grey squirrel and jackdaw (*Corvus monedula*).

## 5. Summary

Sample counts of grey squirrels (*Sciurus carolinensis*) seen per hour may be used for comparing squirrel densities, if the season and speed of the observer are constant. In oak forest the grey squirrel showed a preference for beech; within pure beech there may be competition between squirrel and jackdaw colonies.

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# THE DISTRIBUTION OF AMPHIPODS IN THE SEVERN ESTUARY AND BRISTOL CHANNEL[1]

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(*With 2 Figures in the Text*)

## 1. Introduction

During the course of a biological survey of the intertidal fauna of the Severn Estuary and Bristol Channel a good deal of attention has been paid to the distribution of the abundant and widespread genus of Amphipods—*Gammarus*. As with all the fauna, the actual records of the 54 species of Amphipods have already been presented (Bassindale, 1941). Mr G. M. Spooner has identified all the Amphipods taken in the collections, and it was he who suggested that collections made in summer and winter might show a seasonal shift of populations. The present account deals with the commonest species (excluding sand-hoppers), but particularly with species of *Gammarus* and *Marinogammarus*. Of the *Gammarus* species taken, *G. zaddachi* is the most abundant. There are two notable absentees—*G. duebeni* Lilljeborg and *G. chevreuxi* Sexton.

## 2. Distribution in the Severn Estuary

### (*a*) *General*

Details of the distribution are shown in Fig. 1, where horizontal distribution along the Estuary and Channel is shown on the horizontal axis and tide level is indicated on the vertical axis (the top line representing high-water mark (H.W.M.) and the bottom line low-water mark (L.W.M.)). Horizontal distribution was measured on a map, and tide level was determined by inspection.

Collections were made at each of the stations shown in Fig. 1, by two or three collectors moving over the shore several yards apart. All suitable places were examined—weeds and stones were turned over, streams, pools, soft mud and the channel at L.W.M. were swept by hand net and a spade was used to examine mud and sand deposits. All Amphipods seen were preserved on the spot and identified subsequently by G. M. Spooner. When the group was extremely abundant only 100–200 were taken from each place of abundance. In labelling the tubes during collection, three levels alone were used (H.W., M.T.L. (mean tide level) and L.W.), and the specimens were referred to the

[1] No. 7 of a series on the Biology of the Bristol Channel.

nearest. A circuit of the shore was made and collections taken all the way. The return journey from L.W. to H.W. was usually about 100 yd. away from the outward path. The continuous distribution patches marked on Figs. 1 A and 1 B therefore result from the joining up of these stations.

If in any locality several hundred specimens could be collected in a few minutes and individual stones had 50 or 60 specimens underneath then the group was recorded as abundant. Subsequently it was usually found that the abundance was due to one species. If after some searching at a given level among suitable stones or weeds, a collection of about 100 specimens could be obtained the group was recorded as common, and if as usually happened only one or two species were involved they were both recorded as

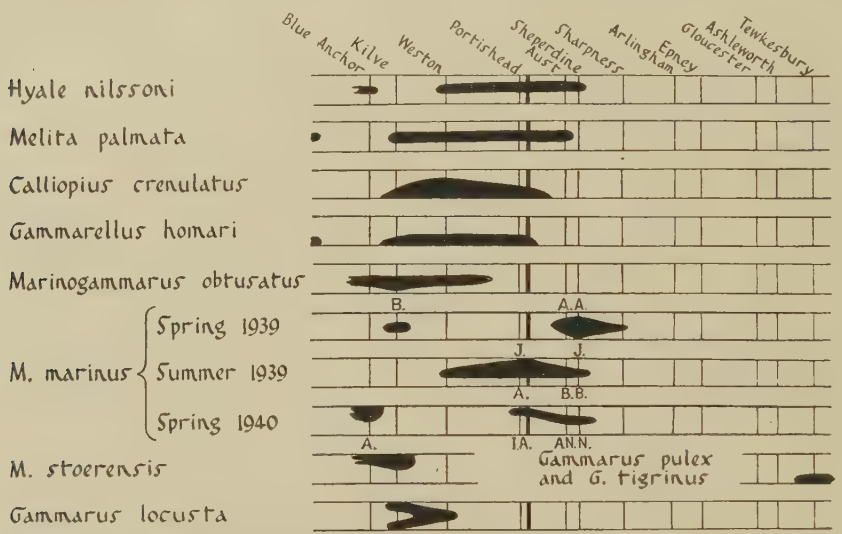


Fig. 1 A. The distribution of certain Amphipods in the Bristol Channel and Severn Estuary. For explanation, see Fig. 1 B.

common. When, after a search of about 50 yd. at a given level only 10 or 20 specimens were obtained all species so collected were recorded as rare. When a species did not appear at all in the dozen or more tubes from any station then it was recorded as absent. All specimens are preserved in the Severn Collection in the Zoology Department, University of Bristol.

The collecting stations were chosen at rocky places where weeds and stones occurred. This was not possible above Arlingham Passage where the banks are all earth slopes. The stations are described in Bassindale (1942).

The salinity data in Fig. 1 have been collected during the present survey, and it is hoped shortly to publish a full account of the physical conditions in the Severn Estuary. The curves shown illustrate the conditions obtaining during an extreme spring tide in ordinary wet and dry weather and similar

data for an extreme neap tide. Except under very unusual conditions all salinities will lie between the curves shown.

Most of the species shown seem to have an estuarine distribution and must be specialized for a brackish water habitat. This applies especially to *Marinogammarus marinus*, *Gammarus zaddachi* and *Calliopius crenulatus*.

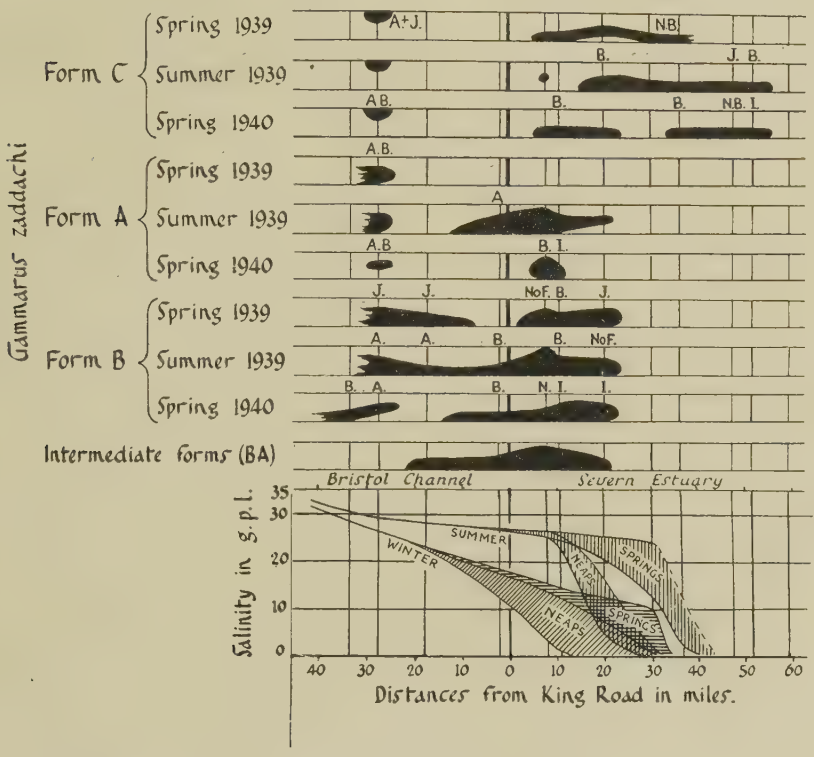


Fig. 1 B. The distribution of *Gammarus zaddachi* and of salinity in the Bristol Channel and Severn Estuary. Place-names are given on Fig. 1 A and distances from King Road (near Avonmouth) on Fig. 1 B. For the Amphipod distributions each strip represents the shore along the estuary—the top line is H.W.M. and the bottom line L.W.M. Letters on the figures have the following meanings: *A*, adults only; *B*, breeding; *F*, females; *I*, inhibited reproduction (i.e. reduced brood plates in adult females); *J*, juveniles only; *M*, males only; *N*, intersexes present; *N.B.* not breeding.

In order to study the seasonal shift of population, the records of *Marinogammarus marinus* and *Gammarus zaddachi* are presented separately for the summer of 1939 (August), and the springs of 1939 (April and May) and 1940 (March and April). Notes on the nature of the population are also given. The main feature is the presence, at the points marked *I*, of specimens showing a condition of inhibited breeding, in which the females were not carrying eggs and the brood plates were of reduced size, and, at the points marked *N*, of

'intersexes', i.e. females without eggs and with subchelae somewhat larger than normal, and males with subchelae somewhat smaller than normal.

It will be noticed that these conditions were observed in three species during the spring of 1940, after the severe frosts of that winter, and that they occur mainly at the upper limit of distribution of the species affected. Spooner has suggested that the extreme cold combined with low salinity produced these anomalies. Collections were made after the mild winter of 1940–1, to see if intersexes had appeared, or whether, as after the mild winter of 1938–9, they were absent; but these new collections have not yet been examined, and it is considered better to present the available data as soon as possible. Experiments are also being carried out on the effect of temperature and salinity on growing *Gammarus* in an attempt to produce the anomalies in the laboratory.

Interesting features of the distributions at Kilve are the recurrence in abundance near H.W.M. of *Gammarus zaddachi* (*Forms A and C*), the elevation of the distribution to M.T.L. of *G. zaddachi* (*Form B*), and the presence of *Marinogammarus stoerensis* Reid (called *Gammarus stoerensis* in Bassindale, 1941). This strong reaction to the presence of fresh water is due to a stream that enters the shore at Kilve and flows over much of the collecting area at this station. The flatworm, *Procerodes ulvae*, is a characteristic and abundant inhabitant near H.W.M. There are also traces of fresh-water influence at Blue Anchor (East), shown by the abundance of *Marinogammarus marinus*, and by the presence of *M. stoerensis* and a single specimen of the polychaete worm, *Nereis diversicolor*; but the stream was not noticed and the shore at H.W.M. gives way to a cliff.

### (*b*) Marinogammarus marinus (*Leach*)

The distribution of *Marinogammarus marinus* is centred on the mid-tide region of the shores from Portishead to Sheperdine. Breeding specimens were rare in the spring of 1939, and in spring, 1940, intersexes and inhibited reproduction were recorded. A curious feature of the spring distribution is the appearance of a large population at M.T.L. at Kilve in 1939, and at H.W.M. at Blue Anchor (and not all at Kilve) in 1940. It seems possible that the lowering of salinity in the estuary during winter, together with the effect of local streams, enabled the species to get a temporary footing, which was lost in the summer of 1939. This would seem to be the only indication of a seasonal change in distribution because, except for the local concentration at Blue Anchor, the distributions in spring 1940 and summer 1939, were identical. In addition the species extended as far up river in spring as in summer 1939, but not so far *seawards*. In the summer, the adult breeding population was found at M.T.L., and a juvenile population near H.W.M. This must mean that young *M. marinus* migrate up the shore after being freed, and then down as they become adult; they then stay at M.T.L. all the year round. Judging from salinity data presented in Fig. 1B, the species seems to live in water of salinity from 28 to below 10 g.p.l.

(*c*) Gammarus zaddachi *Sexton*

When describing *Gammarus zaddachi* in 1912, Sexton pointed out a difference in appearance correlated with the habitat, the animals from fresh water being very hairy, those from the estuary at the other extreme of the species range having many spines but comparatively few hairs. As in her material the difference in appearance was due only to the greater or less development of the cuticle outgrowths, and as all gradations between the two extreme forms were found, she did not consider the distinction sufficient for varietal status.

In the Severn, Spooner has discriminated between three forms of *G. zaddachi* which have been recorded in the fauna list (Bassindale, 1941) as *Saline Varieties A and B* and *Typical Variety*, and all three were attributed to Spooner. Of these, *Saline Variety A* is Sexton's saline form (figured in 1912), common in many British and north European estuaries; *Typical Variety* is her fresh-water form, recorded from a number of localities; but *Saline Variety B* is a distinct form peculiar, so far as is yet known, to the Severn. Despite the description of these forms as 'varieties' in the fauna list, the same objections apply to giving *Saline Variety B* full varietal status as applied to the original saline and fresh-water forms. The new Form B isolated by Spooner does seem to differ in more than cuticular structures (for example, the eye appears to be smaller), but intermediates are common and discrimination is not always possible. It has therefore been decided, in agreement with Sexton, to call the three types Forms A, B and C; Forms A and B being the types occurring in saline waters and Form C the fresh-water type. It must be emphasized that Form B is only provisionally discriminated, and its exact status in relation to Forms A and C is undergoing experimental investigation.

*Gammarus zaddachi* extends in the Severn from Blue Anchor to Ashleworth Ferry, where the water is probably fresh all the time. Form A is not at all common in the Severn and is in large part replaced by Form B. Individuals intermediate between Forms A and B are common and have been recorded from Weston to Sharpness. Form C occupies the uppermost reaches from Aust to Ashleworth, and also recurs at Kilve, where the influence of a fresh-water stream is marked. As with *Marinogammarus marinus* and *M. stoerensis*, intersexes and females showing inhibited development were recorded in spring 1940, at the less saline end of the range of each species. (In the case of *M. stoerensis* the restricted range makes it impossible to tell whether it is the upper or lower end of the salinity range that is affected. It may be noted, however, that the species moved down the shore from H.T.M. to M.T.L. between summer 1939 and spring 1940.)

Form A occurs commonly at Kilve at M.T.L. but not at Weston. It was extremely rare in the estuary after the winter floods and seemed to concentrate at Kilve. In summer it was found from Portishead to Sharpness and

was widespread on the shore at Aust. Inhibited reproduction was present at Sheperdine in spring 1940. The salinity tolerance of this form is similar to that of the commoner Form B.

The commonest Amphipod of the river is undoubtedly *Gammarus zaddachi*, Form B. In summer 1939, there was an abundant population near L.W.M. from Weston to Sheperdine. It showed signs of moving up the shore at Sheperdine and was most abundant at M.T.L. at Sharpness. The population at Sharpness consisted of males and juveniles only, while the population at Weston was of adults only. It would seem that the main breeding zone in summer was from Portishead to Sheperdine, that adults could live seaward of this region, and that juveniles tended to occur upstream of Sheperdine and higher up the shore than adults. In the case of *Marinogammarus marinus* also, juveniles occurred higher up the shore than adults, and the effect on the salinity of the water in which the juveniles lived, as compared with that in which the adults lived, is difficult to assess. It might be the same in the two cases; but the effect on the duration of exposure would be the same—a lengthening.

In spring 1939 the distribution was similar in extent to that of the summer, but the form was much less abundant. At M.T.L. at Sharpness, the population was still of juveniles, and so were the rare specimens taken at Weston and Kilve. No females were taken at Aust and the nucleus of the form was at Sheperdine. The form was much commoner in spring 1940, and showed intersexes and inhibited reproduction at the upper limit of its range. Breeding was, however, in progress lower down at Portishead and Blue Anchor. The optimum salinity conditions seem to lie between 15 and 25 g.p.l., with a tolerance down to 10 g.p.l., or lower for juveniles only.

Records for spring 1939 extend only to Epney, and *Gammarus zaddachi*, Form C was very rare, and was not breeding except at Kilve, where its presence was due to a stream entering the shore. Breeding was taking place in spring 1940, except at Sheperdine and Epney; but at the upper end of the range, about Gloucester and Ashleworth, females showed reduced brood plates. In summer 1939 the form was commoner at Sharpness and Ashleworth than during spring and breeding was taking place. The river between Sharpness and Gloucester is unsuitable for the development of a large *Gammarus* population by reason of the steep earth banks, and the absence of stones or much stable vegetation. From the fact that Form C occurs at Sharpness in summer it must be capable of withstanding salinities up to 25 g.p.l., but its optimum must be considerably lower.

In all three forms, as well as in *Marinogammarus marinus*, the population was more depleted in spring 1939 than in spring 1940, despite the cold winter of 1939–40. It seems possible that the reduced salinity during winter has more effect in reducing the population than has frost—a phenomenon which Fischer-Piette (1931) has already discovered for Ascidians in La Rance.

(*d*) Calliopius crenulatus *Chevreux & Fage*

Chevreux & Fage (1925) record *Calliopius crenulatus* as a rare intertidal species, and it may be that its abundance in the Severn, at Weston and Portishead, is indicative of a brackish water habitat.

(*e*) Gammarellus homari (*Fabricius*)

As with *Calliopius* the present species is described as a rare intertidal form (Chevreux & Fage, 1925), but in the Severn it is common at Weston. It is, however, believed to occur at Porlock Weir, and it is possible that its distribution is sporadic, rather than estuarine.

(*f*) Melita palmata (*Montagu*)

Serventy (1935, p. 291) has suggested that *Melita palmata* is tolerant of estuarine conditions, and that it populates estuaries from its main centres of distribution in the sea. This suggestion is borne out by the distribution in the Severn because, although the species was commoner at Aust than lower down, it occurred at M.T.L. instead of near L.W.M. where it normally occurs (Chevreux & Fage, 1925). It would thereby avoid the more extreme reductions of salinity to which animals living at L.W.M. are subject. Nevertheless, Sexton believes that the species is capable of enduring great extremes of salinity, since it occurs in ditches at Chelson Meadow in company with *Gammarus chevreuxi*. This tolerance is confirmed by Goodhart (1941), who records the species as one of the commonest Amphipods in the estuary of the Afon Water.

(*g*) *The distribution of* Hyale prevosti (*Milne-Edwards*) = H. nilssoni (*Rathke*)

*Hyale prevosti* normally occurs at high water neap tide (H.W.N.T.) level, and it should therefore be able to find a normal environment in an estuary some distance from the sea. It is not surprising to find that, although rare, it extends well into the Severn estuary. It is for similar reasons that the sand-hoppers *Talitrus saltator* and *Orchestia gammarella*, occurring at H.W.M., are found as far up-river as Sharpness.

(*h*) *The distribution of species of* Marinogammarus *spp.*

The habitat and distribution of members of the genus *Marinogammarus* have recently been described by Sexton & Spooner (1940). The distributions of *M. marinus*, *M. obtusatus* and *M. stoerensis* in the Severn do not conflict with these descriptions except for the rarity of *M. marinus* at Kilve and Blue Anchor. It is recorded by Sexton & Spooner (1940, p. 655) that *M. obtusatus* is often locally abundant and may then replace *M. marinus*. It seems possible that this is the case at Kilve and Blue Anchor.

### (*i*) Gammarus locusta (*L.*)

*Gammarus locusta* seems, in the Severn, to be intolerant of reduced salinity, and has occurred very rarely in the collections. It is expected to appear more commonly as the survey is extended seawards. The species *Marinogammarus obtusatus* is shown by Beadle & Cragg (1940*a*, p. 156), from experimental data, to be less tolerant of reduced salinity than *Gammarus locusta*. These authors were informed by Spooner that this relation is supported by the distribution of the two species, and recently published results (see Fig. 2) confirm the point (Goodhart, 1941). It seems, therefore, that *G. locusta* may be restricted in the Severn by factors other than salinity.

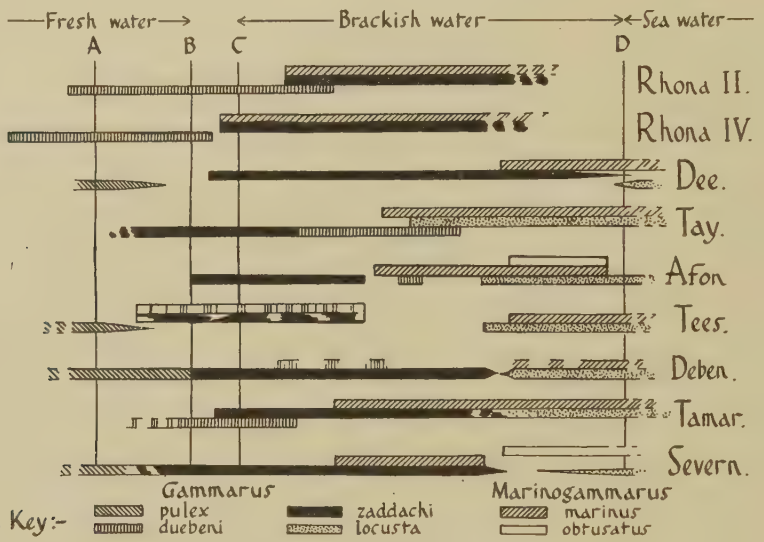


Fig. 2. The relative distributions of species of *Gammarus* and *Marinogammarus* in various estuaries. Tide level is not indicated. The lines *A* to *D* represent: *A*, the limit of tidal action; *B*, the maximum penetration of salt water on spring tides; *C*, the maximum penetration of salt water on neap tides; *D*, the mouth. The diagrams for each estuary are only very approximately comparable with each other.

## 3. A comparison of distributions in the Severn with those in other estuaries

### (*a*) *The salinity ranges of the different species*

From data published in various papers it is possible to estimate approximately the salinity ranges within which species of *Gammarus* and *Marinogammarus* were normally found. The correlations are indirect—that is, the salinity observations were not necessarily made on the collecting site—but a reasonable agreement is obtained (Table 1). Some anomalies do appear, and a closer examination of the differences will be made.

In most of the estuaries considered there is some species of *Gammarus* or *Marinogammarus* in all parts. There is, however, a transition from marine to brackish water species and from brackish water to fresh-water species as the estuary is ascended.

*Gammarus locusta* is a marine species and dies out where the salinity is reduced to below 28 or 25 g.p.l. In the Dee it is so rare where lower salinities have been observed that its normal distribution must be regarded as confined to Greyhope and Nigg Bays, where salinities down to 31 g.p.l. are the lowest recorded. The reasons for its presence in the Tay, where salinities down to 5 g.p.l. are experienced, are not known. The species occurs in salinities down to 21 g.p.l. in a brackish lagoon in Essex, but the conditions there are abnormal (Howes, 1939).

Table 1. *The approximate salinity conditions in which species of* Gammarus *and* Marinogammarus *have been obtained.* (*Abnormal records in heavy type*)

| Species of *Gammarus* and *Marino-gammarus* | Estuary | | | | | | |
|---|---|---|---|---|---|---|---|
| | Severn | Deben (Serventy, 1935) | Tees (Alexander *et al.* 1935) | Tay (Alexander *et al.* 1935) | Tamar (Percival, 1929) | Dee (Milne, 1940*a*) | Afon (Goodhart, 1941) |
| G. pulex | Not to *B** | **To B** | Not to *B* | Not to *B* | Not to *B* | Not to *B* | **Absent** |
| G. duebeni | **Absent** | No details | 28– 0 | 25– 0 | 20– 0 | **Absent** | **Rare** |
| G. zaddachi | 28– 0 | 28– 0 | 28– 0 | **10– 0** | No details | **34– 0** | **16– 0** |
| G. locusta | 35–28 | 35–28 | 35–25 | 35– **5** | No details | 35–12·6 | 35–25 |
| M. marinus | **28**–10 | No details | 35–**23** | 35–10 | 35–10 | 35– **2** | 34–11 |

* See Fig. 2.

*Marinogammarus marinus* occurs in all seven estuaries, but although its salinity range seems to be from 35 (sea water) to about 10 g.p.l., there are four exceptions. In the Tees, the species does not extend into water of so low a salinity as 10 g.p.l., and pollution may be the complicating factor. In the Dee, the species extends to a locality where salinities as low as 2 g.p.l. are recorded, but the Dee estuary has a marked vertical salinity gradient, and general salinity observations must be interpreted with care. *M. marinus* lives at M.T.L., and in the Dee it is probably not subjected to the lowest salinities recorded at the stations concerned except for very short periods. In the Severn, the species does not extend into sea water, and it has been suggested above that this is due to its replacement by *M. obtusatus*. It is not clear whether this replacement of one species by the other is due to 'inter-specific competition' or to unmeasured variations in the environment which favour one species at the expense of the other. The two concepts are different viewpoints of the same phenomenon. The explanation will not, however, suffice for the Afon Water. In this estuary both *M. marinus* and *M. obtusatus* fail to colonize the shores of the Solent beyond the estuary mouth, and Goodhart (1941, p. 320) attributes this to the absence of suitable algae in the Solent.

*M. obtusatus* has not been recorded except from the Afon Water and Severn. This may be due to confusion with *M. marinus*, from which species it has only recently been discriminated (see Sexton & Spooner, 1940).

There has been a good deal of confusion in the past between *Gammarus duebeni* and *G. zaddachi* as well as between these and other species, notably *G. pulex* and *G. locusta*. For this reason it is not always clear which species is meant. (Percival (1929), recorded *G. zaddachi* as *G. locusta* (see Serventy, 1935), and Bassindale (Alexander *et al.* 1935), recorded both *G. zaddachi* and *G. duebeni* in the Tees, as *G. duebeni* (Spooner *in litt.*). The Tay results are, however, correct. For these reasons, Fig. 62 in the Tees Report is incorrect for the Tamar distribution of *G. locusta*, and probably for the Tees distribution of *G. duebeni* and *G. zaddachi*. Similarly, some of the statements near the top of p. 69 may be untrue.) Some information is available and is presented in Table 1.

*G. zaddachi* lives in waters of salinity lower than 28 g.p.l. Its penetration into salinities up to 34 in the Dee is unusual, and an examination of the records (Milne, 1940*a*, p. 118) shows that it is abundant in salinities up to 29, and rare from 29 to 34 g.p.l. The record therefore agrees with those of the other estuaries except for the Tay and Afon. Here the species does not extend into salinities greater than 10 and 16 g.p.l. respectively. It is possible that salinities greater than these are experienced at its lower limit of distribution, but there seems to be no obvious reason for so wide a discrepancy as there is between 10 and 28 g.p.l.

*G. duebeni* can live in water of salinity up to 28 g.p.l., but the maximum range tends to be lower than this. The reason for its absence from the Severn and the Dee and its rarity in the Afon, where it appears to be dying out, is not known. Salinity conditions in parts of the brackish zone of the Severn and Dee are exceptionally severe, but this does not seem to be the case with the Afon.

*G. pulex* is a fresh-water species and has been recorded from the fresh-water reaches of several estuaries.

### (*b*) *The relative distributions of species in different estuaries*

Despite the fact that fairly close agreement is apparent in the records of the salinity ranges of the various species, there is another aspect from which the data may be viewed—that of the distribution of species relative to each other. In Fig. 2 an attempt has been made to illustrate this relative distribution. The fixed points used are four in number: *A*, the point above which the tide wave never affects the river; *B* and *C*, the place of maximum penetration of salt water, which varies from *B* on high spring tides, to *C* on extreme neap tides; *D*, the mouth, which is often indeterminate as, for example, in the Severn. Two new 'estuaries' are shown in the figure and the data for streams II and IV on the island of Rona are from Beadle & Cragg (1940*b*). Salinity measurements are not given, but the points *A*, *B* and *C* are delimited, and although direct comparisons of these very short 'estuaries' (the streams are small and debouch on to the seashore) with the longer types

is not easy, the relative distributions of species is of interest. The Dee is intermediate in character between the Rona type of estuary and the longer types. The Afon Water estuary is also short, but the river is small and the salinity conditions probably correspond more closely than in the Dee with those of the longer estuaries. Another feature of the Afon is that it is subjected to the double high tide characteristic of the Solent into which it discharges.

Of the species considered *G. zaddachi* is perhaps the most important. It is of particular interest because of the different forms which occur as well as because of its abundance in most estuaries. The seaward limit of its distribution varies according to the type of estuary (and, therefore, according to the type of salinity conditions), but it obviously extends nearly to marine conditions. It is the saline form of the species which occupies this part of the range. In the Deben and Severn, and probably in the Tamar (Milne, 1940*b*, Fig. 1), the species extends down to a point just upstream of the limit of penetration of *G. locusta*; but in the Tees, Tay and Afon there is a large gap between the two species. In the Dee they overlap.

At the other end of the range, where the fresh-water *Form C* is usually to be found, the species seems to extend approximately to the point of maximum penetration of salt water (*BC*, Fig. 2). There are two exceptions; in the Tay and Severn the species penetrates into reaches believed to be permanently fresh. The Severn is known to be fed by tributaries of high salt content (see analyses by Cooper in Sexton, 1939), but, until complete analyses of the fresh water of all the rivers are available, no explanation can be advanced as to why *G. zaddachi* extends into fresh water in some estuaries and not in others, since the species is known to be capable of living all its life in fresh-water rivers and lakes (Sexton *in litt.*).

Although the fresh-water *G. pulex* has only been recorded from a few of the estuaries, and does not occur on Rona or in the Afon Water, it is apparent that its distribution differs in relation to the limit of salt-water penetration (*B*). In the Deben, Serventy (1935) showed how *G. pulex* replaced *G. zaddachi* very suddenly just above the point *B*, thus indicating that it might be expected to extend down to that limit in other estuaries. But this is not the case. The Deben is an exception and, although records of the species may not have been made, it is clear that *G. pulex* does not extend down to *B* in five of the estuaries shown in Table 1. This inexplicable circumstance merely emphasizes the need for analyses of river water, of which only those of the Dee (Milne, 1940*a*), and the Tees (Butcher *et al.* 1937) are available.

The second brackish water species, which occurs abundantly in estuaries, is *G. duebeni*. This is a species which has successfully colonized fresh water in Ireland and elsewhere, but on Rona it remains in the lowest reaches only—and for no apparent reason (Beadle & Cragg, 1940*b*). In the Tees, Deben, and Tamar, the range of the species overlaps that of *G. zaddachi*, but it tends to occur upstream of *G. zaddachi* in the Tamar, as on Rona. It is surprising, therefore, to find the species downstream of *G. zaddachi* in the Tay, and not

extending into fresh water. This is the second anomaly noted in the Tay. The species also occurs downstream of *G. zaddachi* in the Afon, but it is rare and appears to be dying out, so that comparisons cannot safely be made.

Among the marine species, *Marinogammarus marinus* penetrates farthest, and its range overlaps considerably the distribution of other species; but since it occurs at M.T.L. it does not normally come into direct competition with them, because, except for *M. obtusatus*, they occur at L.W.M. In the Dee it seems probable that *Gammarus zaddachi* does occur above L.W.M., since it is taken with *Marinogammarus marinus*. This may be a response to the vertical salinity gradient of the Dee and is comparable with the upshore movement of the species at Sharpness in the Severn. *M. marinus* penetrates to about the place where *Gammarus duebeni* appears.

*Marinogammarus obtusatus* has only recently been discriminated from *M. marinus*, and the replacement in the Severn of one species by the other (see above), is paralleled in the Afon where, although the distributions of the two species overlap, the two never occur together. The same phenomenon will doubtless be recorded from other estuaries as *M. obtusatus* becomes more widely recognized.

In the case of the marine *Gammarus locusta*, it is clear that the species normally gives way to *G. zaddachi*, where the salinity falls to below 28 g.p.l. In the Deben, at Methersgate, there is a short gap between the point where *G. locusta* dies out and *G. zaddachi* appears. A comparable zone is found in the Severn, at Blue Anchor and Kilve, where the salinity conditions appear to be the same as those at Methersgate. The distributions of these species in the Tamar is apparently similar (Milne, 1940*b*, Fig. 1), and in the Dee, with its unusual salinity conditions, the species overlap; but large gaps appear in the Tees, Tay and Afon between the upper limit of *G. locusta* and the lower limit of *G. zaddachi*. In the Tees this may be due to pollution, but in the Tay the gap, which is actually occupied by *G. duebeni*, is merely one more of the anomalies of distribution in this estuary, for which an explanation is difficult to find. A similar gap appears in the Afon, and the rare specimens of *G. duebeni* collected occur in the gap just as in the Tay. The presence of the gap is due to the fact that *G. zaddachi* does not penetrate into such high salinities as normally (see Table 1), but why *G. duebeni* should come downstream to fill the gap is not clear. There is a possibility that no saline variety of *G. zaddachi* occurs in the Tay and Afon.

## 4. Acknowledgements

Mr G. M. Spooner expended much time in identifying all the Amphipods from the Severn collections and, after he left Plymouth, Mrs E. W. Sexton kindly read through the manuscript. The genus *Gammarus* has recently undergone extension and revision by these two workers, and I am very grateful for their expert assistance.

As with the whole Severn survey, the work embodied in the present paper has benefited by the continued suggestions and encouragement of Prof. C. M. Yonge. I should also like to express my thanks to the Leverhulme Trustees for their assistance to the Survey.

## 5. SUMMARY

1. The distribution of the commonest Amphipods in the Severn Estuary is described:

(*a*) *Gammarus zaddachi* is the commonest species and occurs in three forms, A, B, and C. Forms A and B are closely similar and live in fairly salt water. Form C extends into fresh water. These forms were incorrectly called 'Varieties' in Bassindale (1941).

(*b*) Seasonal changes are not outstanding. There is a greater abundance of specimens in summer and a tendency for juveniles alone to occupy the less saline end of the range in winter.

(*c*) In three species there were intersexes and females showing inhibited breeding after the severe winter of 1939–40. These occurred at the less saline end of the range of the species concerned.

(*d*) The recurrence of brackish water forms at Kilve is attributed to the influence of a fresh-water stream which enters the shore there.

(*e*) *Gammarus duebeni* and *G. chevreuxi* are absent.

2. The known distribution of *Gammarus* and *Marinogammarus* in this and other estuaries is compared:

(*a*) The salinity ranges of five species of *Gammarus* and *Marinogammarus* are given (Table 1) and exceptional records are discussed.

(*b*) The Tay proves exceptional in the following respects: *Gammarus duebeni* occurs seaward of *G. zaddachi* and does not enter regions which are always fresh; *G. zaddachi* does enter regions which are believed to be always fresh; the distribution of *Marinogammarus marinus* overlaps that of *Gammarus duebeni*; *G. locusta* penetrates farther from the sea than expected, but does not reach the *G. zaddachi* zone, which is farther upstream than normal. The Afon Water shows some of these characters.

(*c*) Much variation occurs in the distribution of the several species of *Gammarus* and *Marinogammarus*, notably in the Tay, and detailed observation of physical conditions on the actual collecting sites will be necessary to elucidate these peculiarities.

3. The following description summarizes the whole of the available observations, when certain exceptional records are neglected:

*Gammarus pulex* is a species which is intolerant of dissolved salt or of a pronounced tidal rhythm—at any rate when in competition with other species—and it does not penetrate far into the tidal fresh-water reaches at the head of the estuary.

*G. duebeni* lives in water of low salinity but tolerates salinities up to 20 or 25 g.p.l. It occurs from the zone of tidal fresh water, through the transition zone, into water which is nearly always brackish. Here its distribution overlaps that of *G. zaddachi*.

*G. zaddachi* lives in salinities below 28 g.p.l. and so extends from the zone which is not permanently fresh, i.e. from the zone of maximum penetration of salt water, to a point near the mouth where it is replaced by *G. locusta*.

*G. locusta* lives in waters of salinity greater than 28 g.p.l. and so occurs near the mouth only.

*Marinogammarus marinus* occurs at mean tide level and lives in zones where the salinity does not fall below 10 g.p.l. It extends from the mouth to a point somewhat below the seaward end of the *Gammarus duebeni* zone. Near the mouth it may be replaced by *Marinogammarus obtusatus*, which is believed to be a markedly stenohaline species.

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# REVIEWS

## *THE JOURNAL OF ECOLOGY*

(Vol. 30, No. 1, February 1942)

THIS number contains nine original papers (including two contributions to the Biological Flora of the British Isles), two reviews and a list of ecological papers. It is concluded by a report of the activities of the British Ecological Society. Most of the original papers deal with work carried out before the war began, and though the rate of supply is falling off, it has been possible, especially with the collaboration of overseas workers, to maintain the character of the *Journal*.

Two papers by C. H. Mortimer, important for general biologists and limnologists, deal with the exchange of dissolved substances between the underlying mud and the water of lakes. They show that the water may gain in dissolved substances of nutritive importance during periods of oxygen deficiency and also describe new methods of measuring the phenomena in deep water.

A long survey of the vegetation communities of East Africa is communicated by C. H. N. Jackson. This has been largely compiled from reports and field notes by the late B. D. Burtt, supplemented from the editor's experience. It is published as part of a Burtt-Swynnerton Memorial, organized by friends and colleagues, which has made exceptional and valuable illustration possible. Also dealing with overseas vegetation is an account of the vegetation of islands in the Indian Ocean (north of Madagascar) by D. Vesey Fitzgerald. These are coral islands raised above sea-level and now undergoing denudation resulting in a definite series of habitats.

Dealing with British vegetation are two papers. One, on ecological aspects of peat accumulation by J. L. Harley and E. W. Yemm, deals with the plant ecology of Thornton Mire, a small area of peat in Wensleydale, with some account of its stratigraphy. Ian Hepburn gives an account of grasslands developed over the sites of ancient quarries at Barnack. These were worked for oolite in Roman times and have probably been unused since about A.D. 1500.

The remaining papers are an appreciation of the late G. E. Nicholls by N. Polunin, and contributions to the Biological Flora of the British Isles. The latter deal with *Cladium mariscus*, by V. M. Conway; and *Zostera*, including *Z. marina* and *Z. Hornemanniana*, by T. G. Tutin. The second is of interest in connexion with the decrease in abundance of this genus in many tidal waters. Reviews are the customary one of *The Journal of Animal Ecology* and one of V. J. Chapman's text-book on Algae. A list of recent papers on plant ecology is also given.

W. H. PEARSALL

## PREDATORS IN NATURE RESERVES

**Adolph Murie (1940).** *Fauna of the National Parks of the United States: Ecology of the coyote in the Yellowstone.* U.S. Dep. Interior, Nat. Park Service, Fauna Series, No. 4: 1–206. 57 illustrations, including a map. Price 30 cents.

In 1933 it was suggested[1] that a National Park policy for the vertebrates should include these principles: 'That no management measure or other interference with biotic relationships shall be undertaken prior to a properly conducted investigation....' 'That no native

[1] Wright, G. M., Dixon, J. S. & Thompson, B. H. (1933). 'Fauna of the National Parks of the United States: A preliminary survey of faunal relations in National Parks.' U.S. Dep. Interior, Nat. Park Service, Fauna Series, No. 1: 147.

predator shall be destroyed on account of its normal utilization of any other park animal....' Following this policy coyote control in the Yellowstone was stopped in 1935 and from 1937 to 1939 Dr Murie studied this, almost the last of the large carnivores: for cougar, wolf, red fox, wolverine, bobcat and lynx had been hunted, trapped and poisoned almost to extinction.

Yellowstone National Park is an area of 3500 sq. miles of plateau and mountain at 5000–10,000 ft. altitude. Elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), antelope (*Antilocapra americana*) and bighorn (*Ovis canadensis*) are the principal ungulates. These and a great many other animals, from bison to Mormon crickets, play a part in the ecology of the coyote. A study that covers so many species, so large an area, and so short a time will obviously fail unless a proper perspective is maintained; and here Dr Murie has undoubtedly concentrated on the right forms of census and analysis.

From over 5000 coyote droppings he learned the type of food and its importance in the diet. Next the effects of predation on the important species had to be determined by studying the mortality among their young (chiefly through counts of young-adult ratios). Then other causes of mortality had to be fixed.

In brief it was concluded that elk were overcrowded anyway (and coyotes did not keep them down); that deer, which had increased steadily since the end of predator control, were also suffering from over-grazed pastures; that further increase of antelope would probably be undesirable because of lack of winter range; and that all these three species seriously competed for food with the bighorn. Predation of the young by coyotes both in terms of absolute numbers killed and relative to other causes of mortality was almost negligible. In the form of carrion, however, these animals provide the coyote with its most important winter source of food, which at other times of the year is chiefly rodents. No evidence could be found that the rare trumpeter swan (*Cygnus buccinator*) suffered from attacks by coyotes; but a serious threat to their increase and spread appeared to be the ingestion of lead shot from the bottoms of lakes.

To the unscientific, the sight of a predator's work is probably the most obvious of the numerous and complex factors which limit a prey population. It is therefore not surprising that in many parts of the world more effort is put into predator control than into other forms of conservation. This study shows quite clearly that in the Yellowstone, energy directed against this natural predator would, at best, be wasted. It is to be hoped that National Parks schemes in other countries will be guided by principles as high as those of the United States National Park Service.

DENNIS CHITTY

# NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

**This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, University Museum, Oxford.**

**Duplicate copies of these notices can be obtained separately in stiff covers (printed on one side of the page to allow them to be cut out for pasting on index cards) from the Cambridge University Press, Bentley House, 200 Euston Road, N.W.1, or through a bookseller, price 3*s.* 6*d.* per annum post free (in two sets, May and November).**

**Abstracting has been done by H. F. Barnes, D. H. Chitty, C. Elton, B. M. Hobby, M. Mare, Barrington Moore, F. T. K. Pentelow, H. N. Southern and U. Wykes.**

**Within each section the groups are arranged in the order of the animal kingdom, beginning with mammals (in the section on parasites the hosts are classified in this order). Papers dealing with technical methods are dealt with in the appropriate sections.**

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## 1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

### (*a*) Marine and brackish

**Matthews, L. H. (1941).** 'Studies on the biology of the Bristol Channel. VI. The marine mammals of the Bristol Channel.' Proc. Bristol Nat. Soc. 9: 231–50.

General notes on seals and whales. All species except the common seal and the porpoise are casuals. The common seal (*Phoca vitulina*) has recently started a small breeding colony at the Denny, off Portishead.

**Fisher, J. & Waterson, G. (1941).** 'The breeding distribution, history and population of the fulmar (*Fulmarus glacialis*) in the British Isles.' J. Anim. Ecol. 10: 204–72.

An investigation by the British Trust for Ornithology from 1934 to 1939, incorporating previous published accounts. Breeding only at St Kilda in 1878, the fulmar has spread in five main directions until, in 1939, there were, outside of St Kilda, 40,500 breeding pairs in 208 nesting colonies, and 61 other colonies apparently not yet breeding. Its spread in Britain is not due to decrease in fulmar killing by man on St Kilda, but to a biological change not understood, and it will continue. The fulmar is a Palearctic breeding species, having a life span of over 12 years, with a present southward limit along the 60° F. July isotherm, and a preference for islands. Its nesting site differs from that of other cliff-nesting birds in its range. Large colonies arrive earlier than small colonies and produce more young in proportion to the number of breeding pairs. The Atlantic fulmar has no predators except man. It is primarily a plankton feeder, but also eats any other oily matter it can get. The paper is well illustrated by maps and photos.

**Lloyd, A. J. (1941).** 'Studies on the biology of the Bristol Channel. V. The marine fish fauna of the southern shores of the Bristol Channel.' Proc. Bristol Nat. Soc. 9: 202–30.

General fish fauna list with notes on abundance and marketing.

**Fowell, R. R. (1939).** 'Living communities harboured by the oar weeds (*Laminaria*).' Proc. Swansea Sci. Fld Nat. Soc. 2: 92–103.

Notes on animals found in association with *Laminaria digitata*, *L. saccharina* and *L. cloustoni* in Langland Bay, Glamorgan.

**Bassindale, R. (1941).** 'Studies on the biology of the Bristol Channel. IV. The invertebrate fauna of the southern shores of the Bristol Channel and Severn Estuary.' Proc. Bristol Nat. Soc. 9: 143–201.

General fauna list with some notes on associations and abundance.

**Kerr, J. G. (1941).** 'Hydrological and biological studies of Loch Sween.' Nature, Lond. 148: 314.

Loch Sween, Argyle, affords excellent opportunities for marine biological research. Investigations deserving special attention are: (1) the hydrography of the Loch, especially the rise and fall of its water level, and (2) the origin of the fine silt accumulating in the Loch, which is inimical to the oysters. Is a portion of this silt contributed by the rich planktonic and other fauna?

**MacDonald, R. (1941).** 'The Crustacea, Cirripedia, of Co. Down.' Ann. Mag. Nat. Hist. 7: 503–6.

A list of species, giving exact localities as far as possible. A brief comparison is made with the Cirripede fauna of the Isle of Man.

**Williams, G. & Needham, A. E. (1941).** 'Metric variations in populations of *Carcinus moenas*.' J. Mar. Biol. Ass. U.K. 25: 261–81.

Allometric growth of the carapace of male shore crabs had previously been shown to occur at Plymouth. The phenomenon was analysed in laboratory-reared crabs and over a period of three years in three different Irish habitats. As in the previous observations, there was a significant decline in the ratio of the frontal width to the carapace length for crabs of the same size in successive years, but such a decline could not be continued indefinitely. The yearly difference was much more marked than local differences. It is tentatively suggested that annual differences might be due to some general hydrographical effect on the larvae. Local differences were only significant among the larger crabs, suggesting a slight effect of some continually operating factor. Local differences could not be correlated with silt in the habitat. It is suggested that local races are less easily developed in marine forms having free-swimming larvae than in terrestrial species.

**Panikkar, N. K. (1941).** 'Osmoregulation in some Palaemonid prawns.' J. Mar. Biol. Ass. U.K. 25: 317–59.

*Palaemonetes varians* occurs in fresh and brackish water, *Leander squilla* in estuarine and marine habitats and *L. serratus* usually only in the sea. All these species can live satisfactorily in the slightly concentrated sea water of an aquarium circulation and were found to survive for varying lengths of time in much diluted sea water. All species showed an appreciable osmotic independence in both hypertonic and hypotonic media; *Palaemonetes varians* was practically homoiosmotic over a wide range, and *Leander serratus*, while hypotonic in its normal habitat, showed least ability to maintain a constant osmotic pressure in varied media. Seasonal changes in the salinity of its brackish water habitat caused slight corresponding variations in the osmotic pressure of the blood of *Palaemonetes varians*. The physiology of osmoregulation was investigated in detail. It is suggested that this group of Crustacea gained their osmotic independence in fresh water and that *Leander squilla* and *L. serratus* are secondarily marine. Comparisons are made with the osmotic behaviour, in relation to distribution and breeding habits, of other Crustacea.

**Reid, D. M. (1940).** 'Three species of Amphipoda (Crustacea) new to Britain.' Ann. Mag. Nat. Hist. 6: 335–7.

*Gammarus olivii*, from slightly brackish water in the river Afon Water, Hampshire, a Mediterranean species. *G. lacustris*, from fresh-water lochs in Caithness and Sutherland, previously known from the Outer Hebrides, Norway, Sweden, Denmark and Germany. *Hyale perieri*, from intertidal rock pools in north Cornwall, previously known from the Atlantic seaboard of Europe and North America and from the Mediterranean.

**Reid, D. M. (1941).** 'The Amphipod fauna of Oldany Harbour, Sutherland.' J. Anim. Ecol. 10: 296–305.

Among the Amphipods in an almost land-locked shallow lagoon with a shell sand bottom and a deeper basin with a mud and rock bottom, were several species associated with greater depth further south.

**Goodhart, C. B. (1941).** 'The ecology of the Amphipoda in a small estuary in Hampshire.' J. Anim. Ecol. 10: 306–22.

In the estuary of the Afon Water, 18 species of Amphipoda were collected. Salinity is the most important factor, and four groups are recognized based on toleration of different salinities. The nature of the substratum limits the occurrence of some species in water of favourable salinity.

**Hardy, A. C. (1941).** 'Continuous plankton records: general introduction to the 1938–39 survey.' Hull Bull. Mar. Ecol. 2: 1–17.

The survey of phytoplankton and zooplankton in the North Sea was extended as far north as Bergen, and an oceanic line started across the entrance to the Faeroe-Shetland Channel. Eleven lines were in operation, most of which had points of intersection, thereby providing on the whole confirmatory evidence of the usefulness of the method. A summary list of records is given.

**Holmes, W. (1940).** 'The colour changes and colour patterns of *Sepia officinalis* L.' Proc. Zool. Soc. Lond. A, 110: 17–35.

A very complete account of the colour reactions to different backgrounds. *Sepia* is unique in being able to change very complicated patterns in as small a time as two-thirds of a second. This quick change probably protects the species by confusing and frightening the predator.

**Brambell, F. W. R. & Goodhart, C. B. (1941).** '*Saccoglossus horsti* sp.n., an Enteropneust occurring in the Solent.' J. Mar. Biol. Ass. U.K. 25: 283–301.

A new species of Hemichordate is locally common in deep grey mud about low water mark and in certain pools higher on the shore. Specimens are 1 ft. or more in length. A full description of external features and anatomy, with numerous figures, is given.

**Brambell, F. W. R. (1941).** 'The occurrence of *Aequorea vitrina* Gosse in the Menai Straits.' Northw. Nat. 16: 28–9.

Records the fact that three specimens of this Hydromedusan were collected in August from shallow water at low tide near Bangor.

**Moore, H. B. (1941).** 'A wire-angle indicator for use when towing plankton nets.' J. Mar. Biol. Ass. U.K. 25: 419–22.

A large dial registers continuously the angle of the wire, which can be regulated to within $\pm 2°$, thus maintaining a horizontal tow.

(*b*) Fresh water

**Ticehurst, C. B. (1940).** 'Notes on the moorhen (*Gallinula chloropus chloropus*).' Ibis, 4: 539–42.

Of 45 picked up dead in cold weather, 58% were males, and 42% were adults. They weighed from three-quarters to half normal weight.

**Allen, K. R. (1941).** 'Studies on the biology of the early stages of the salmon (*Salmo salar*). 3. Growth in the Thurso river system, Caithness.' J. Anim. Ecol. 10: 273–95.

Between August 1937 and October 1938 the same methods that had been used on the river Eden (**Allen, K. R.**, J. Anim. Ecol. 9: 1–23 and 10: 47–76) were used on three tributaries of the Thurso river. The results agree with those of the earlier work as to seasonal variations in the growth rate and related phenomena, and further support the hypothesis that 7° C. is the critical temperature determining the activities and growth of young salmon in Britain. The growth in one year depends on the amount of available food, the date at which the temperature rises to 7° C. and unknown factors determining the rate of growth during the slow period, and the length of this period.

**Moon, H. P. & Green, F. H. W. (1940).** 'Water meadows in southern England.' The Land of Britain, the report of the land utilisation survey of Britain, Part 89, Hampshire: 373–90.

Water from a river is led in a series of ditches through fields, overflows down the slope to another series of ditches which leads it back to the river lower down. Present agricultural conditions have very largely led to neglect of these meadows which used to produce luxuriant grass for grazing and hay. They have a rich invertebrate fauna which gets washed down to the river and could profitably be developed as trout or salmon hatcheries.

**Macan, T. T. & Macfadyen, A. (1941).** 'The water bugs of dewponds.' J. Anim. Ecol. 10: 156–83.

In 50 collections in Wiltshire and Sussex from dewponds, characterized by isolation and calcareous water, and varying from much pollution by sheep and cattle to no pollution, 14 species of Corixidae were found, of which four are common. These four have different requirements as to vegetation and degree of pollution. The dewpond fauna differs from that of other small isolated but non-calcareous bodies of water.

**Fraser, F. C. (1941).** 'Historical, biological and ecological notes on *Ischnura pumilio* (Charp.) (Odonata).' J. Soc. Brit. Ent. 2: 110–16.

This rare dragonfly is carefully compared with *I. elegans* with which it is sometimes confused. It frequents bog-land, especially runnels or brisk seepages on hill-sides meandering down into bogs.

**Kimmins, D. E. (1941).** 'Under-water emergence of the sub-imago of *Heptagenia lateralis* (Curtis) (Ephemeroptera).' Entomologist, 74: 169–70.

Full-grown nymphs of this mayfly come to the surface and gulp in air which fills the gut and is forced between nymphal and sub-imaginal skins. The 'dun' emerges below water. This is considered an adaptation protecting the transforming nymph from disturbances which would be encountered at the margins of lakes.

**Macan, T. T. & Macan, Z. (1940).** 'Preliminary note on the Ephemeroptera and Plecoptera of the Hampshire Avon and its tributaries.' J. Soc. Brit. Ent. 2: 53–61.

Collections were made from the main channels, from New Forest tributaries (acid), from chalk tributaries (alkaline) and from a Reading Beds tributary. Though the collections were insufficient for ecological purposes, they show a contrast between a chalk and a New Forest tributary, and a rich fauna in the Reading Beds tributary.

**Panikkar, N. K. (1941).** 'Osmotic behaviour of the fairy shrimp *Chirocephalus diaphanus* Prévost.' J. Exp. Biol. 18: 110–14.

*Chirocephalus* can absorb ions from tap water, thereby maintaining normal osmotic concentration of its blood. In glass-distilled water the concentration gradually falls.

**Scourfield, D. J. (1941).** 'Discovery of *Mysis relicta* in Ennerdale.' Nature, Lond. 148: 228.

This is the first record of this 'relict' crustacean for Great Britain. Following the discovery of *Limnocalanus macrurus*, also probably modified from a marine species, in the same waters, 360 ft. above sea-level, this calls for renewed consideration by zoologists and geologists.

**Taylor, C. B. (1940).** 'Bacteriology of fresh water. I. Distribution of bacteria in English lakes.' J. Hyg., Camb. 40: 616–40.

Increase in the number of bacteria, due to the main river flowing into Lake Windermere, extended for 200 m. offshore. Vertical distribution during the period of stratification (summer) showed decreasing numbers with depth in the epilimnion, but approximately the same numbers at all depths below the thermocline. During the winter period of circulation, numbers were approximately the same at all depths at any one time. Depletion of dissolved oxygen did not stimulate anaerobic bacteria, most of which were facultative. Fluctuations in numbers were correlated with the rainfall of the week preceding sampling. Temperature and concentration of inorganic substances showed no relation to fluctuations. There was no apparent decrease in numbers due to sunlight.

**Taylor, C. B. (1941).** 'Bacteriology of fresh water. II. The distribution and types of coliform bacteria in lakes and streams.' J. Hyg., Camb. 41: 17–38.

Coliform bacteria were, in general, much more numerous in summer than in winter; and in relatively unpolluted waters increased with the water level, whereas in polluted waters they decreased with increased inflow owing to dilution. Large weekly fluctuations in numbers were not related to previous rainfall. In the relatively pure waters of Lake Thirlmere and its inflows, *Bacterium coli* type I made up 86 and 98% respectively of the coliform bacteria, whereas in the relatively impure waters of Windermere and Esthwaite Water it was only 39 and 37% respectively, owing to the larger proportions of *B. aerogenes* type I and others of the I.A.C. group. Actual counts of coliform bacteria were much lower in Thirlmere. Nearly 300 cultures were isolated from positive tubes of MacConkey broth and their relation to the coliform group studied.

**Mortimer, C. H. (1940).** 'An apparatus for obtaining water from different depths for bacteriological examination.' J. Hyg., Camb. 40: 641–6.

A thick-walled bottle of 1 l. capacity, fitted with a straight inlet tube and an air outlet tube bent into a double loop, both closed by a single stopper, is fitted into a frame on which is a spring, tied to the stopper and held extended by a thin steel cable attached to a catch which is released by a messenger at the desired depth. The bent air outlet tube prevents entry of water in raising the bottle. For oxygen determinations a second bottle is suggested through which the water must pass into the collecting bottle.

(c) Land

**Tetley, H. (1941).** 'Land mammals of the Bristol district.' Proc. Bristol Nat. Soc. 9: 100–42.

General survey of the land mammals with notes on colour variation and average dimensions.

**Deal, J. (1941).** 'The temperature preferendum of certain insects.' J. Anim. Ecol. 10: 323–56.

The preferendum, as contrasted with the optimum, is the temperature to which an insect moves if given its choice in a temperature gradient. The apparatus used gave a range from 10 to 35° C., with 1° C. in every 4 cm. Relative humidity varied inversely with temperature, except when food was given, when it was practically uniform. Each experiment covered 3 days, and controls of 1 day gave the random distribution. In all, 23 species of insects, representing different habitats of economic importance, were tested. Preference represented a range rather than a point, and showed a narrower range with food than without food. In general, all insects experimented with showed a definite temperature preference.

**Krogh, A. & Zeuthen, E. (1941).** 'The mechanism of flight in some insects.' J. Exp. Biol. 18: 1–10.

Butterflies, moths, bumble bees and Lamellicorn beetles, which at rest have a temperature about the same as their environment, have first to raise the temperature of their wing muscles before they can fly. This is done by vibratory movements of the wings.

**Evans, A. C. (1941).** 'Physiological relationships between insects and their host plants. II. A preliminary study of the effects of aphides on the chemical composition of cabbage and field bean.' Ann. Appl. Biol. 28: 368–71.

Infestation of cabbage by *Brevicoryne brassicae* caused a marked decrease in the amount of carbohydrate synthesized, but infestation by *Aphis fabae* on field beans did not have any great effect on the chemical composition of the plant.

**Williamson, K. & Cowin, W. S. (1941).** 'Some Wiltshire insects.' Entomologist, 74: 174–6.

Briefly records habitats.

**Leeds, H. A. (1941).** 'Butterfly collecting in Wood Walton, Hunts., area during 1941.' Ent. Rec. 53: 128–30.

Includes some ecological details.

**Wiltshire, E. P. (1941).** 'The phenological classification of Palaearctic Lepidoptera. A preliminary essay.' Ent. Rec. 53: 101–6.

Butterflies and moths are arranged in three groups: A, continuously brooded species; B, two brooded species; C, single brooded species, with seasonable subdivisions. See also **A. J. Wightman (1941)**, ibid. 53: 130–2.

**Reid, J. A. (1941).** 'A note on oviposition preferences in *Smerinthus populi* (L.) (Lepidoptera, Sphingidae).' Proc. R. Ent. Soc. Lond. (A), 16: 91–2.

A single female of the poplar hawk-moth showed a strong preference to oviposit on *Populus* rather than on *Salix*. It preferred white poplar to balsam poplar and aspen.

**Carter, N. W. J. (1941).** 'Diurnal flight of Taeniocampids.' Entomologist, 74: 211.

Mentions several instances of day-flying moths of the genus *Taeniocampa*.

**Bretherton, R. F. (1941).** 'Diurnal flight of *Taeniocampa cruda*.' Entomologist, 74: 157.

This species of moth was feeding at sallows and flying in bright sunshine.

**de Worms, C. G. M. (1941).** 'Time of flight of *Hemaris tityus* (*bombyliformis*).' Entomologist, 74: 157.

States that the bee-hawk moth flies from 12.0 noon to 4.30 p.m.

**de Worms, C. G. M. (1941).** 'Larvae of *Cirrhodia xerampelina*.' Entomologist, 74: 165–6.

The larvae of this moth are best trapped in wide pieces of sacking strapped round ash trees about 5 ft. from the ground during May.

**Beirne, B. P. (1941).** 'A list of the microlepidoptera of Ireland.' Proc. R. Irish Acad. 47 B: 53–147.

The last general list was published in 1901. 709 or 54·2% of the British Microlepidoptera have been recorded from Ireland, but of these 105 are considered incorrect or doubtful, leaving only 46·2% definitely recorded. 65% of the British Macrolepidoptera have been recorded.

**Bentley, E. W., Gunn, D. L. & Ewer, D. W. (1941).** 'The biology and behaviour of *Ptinus tectus* Boie (Coleoptera, Ptinidae), a pest of stored products. I. The daily rhythm of locomotory activity, especially in relation to light and temperature.' J. Exp. Biol. 18: 182–95.

Changes in position of spider beetles in 2½ l. jars were observed for a random instant every 15 min. for 4–5 days. Activity was greatest in the dark (actually neon lights were used) and the rhythm could be reversed by interchanging the times of light and darkness or obliterated in continuous light at constant temperatures. In continuous light but with fluctuating temperatures greatest activity occurred while the temperatures were falling.

**Crombie, A. C. (1941).** 'On oviposition, olfactory conditioning and host selection in *Rhizopertha dominica* Fab. (Insecta, Coleoptera).' J. Exp. Biol. 18: 62–79.

This 'Australian wheat weevil' finds its food chiefly by smell. In the selection of a site for oviposition touch is of considerable importance; but in the absence of olfactory stimulation as well, e.g. in plaster of Paris wheat grains, the number of eggs laid was about 5% of the total laid in proper wheat grains or in grains made of plaster of Paris and wheat flour.

**Donisthorpe, H. (1941).** 'The distribution of *Lucanus cervus* L. (Col., Lucanidae) in Britain.' Ent. Mon. Mag. 77: 198–9.

Gives map of the distribution of the stag-beetle. Its most northerly record is from Derbyshire.

**Fisher, R. C. (1941).** 'Studies of the biology of the death-watch beetle, *Xestobium rufovillosum* De G. IV. The effect of type and extent of fungal decay in timber upon the rate of development of the insect.' Ann. Appl. Biol. 28: 244–60.

The rate of boring and development of the larvae increases as the extent of decay by fungi of the brown or white rot types increases. Changes in density and mechanical strength of timber resulting from fungal attack also affect the rate of larval development and the duration of the life cycle. Under favourable conditions of temperature and humidity, the degree of susceptibility of a suitable timber species to attack by the death-watch beetle is determined primarily by the extent of fungal decay in it.

**Massee, A. M. (1941).** 'The Hemiptera-Homoptera (Auchenorhyncha) associated with cultivated fruits.' J. Soc. Brit. Ent. 2: 99–109.

Gives a list of leafhoppers and froghoppers associated with cultivated fruits and hops arranged under host plants.

**Greenslade, R. M. (1941).** 'Strawberry aphis and the weather in 1940.' Rep. E. Malling Res. Sta. 1940: 65–6.

Although nearly exterminated by the severe weather of January and February, it was just as numerous as usual by September.

**Coe, R. L. (1941).** 'Some breeding records of British Tipulidae (Dipt.).' Ent. Mon. Mag. 77: 172.

Breeding habits of 17 species of crane-flies.

**Hardy, E. (1941).** 'Reactions of certain Diptera to colours.' Ent. Mon. Mag. 77: 169–71.

Review of the literature

**Greenslade, R. M. (1941).** 'The black currant leaf midge *Dasyneura tetensi* (Rübs.).' Rep. E. Malling Res. Sta. 1940: 66–71.

Host plants, effect of wind on adults and number of generations.

**Niblett, M. (1941).** 'Notes on some gall-causing Cecidomyidae: I.' Entomologist, 74: 221–4.

**Niblett, M. (1941).** 'Notes on the Cynipid genera *Cynips*, *Biorhiza* and *Megaptera*.' Entomologist, 74: 153–7.

Notes on galls and their makers.

**Niblett, M. (1940).** 'Some notes on the Cynipid *Andricus*.—I.' Entomologist, 73: 206–10.

Breeding notes on galls of oaks and distributional records chiefly from Surrey.

**Kloet, G. S. (1941).** 'A new observation nest for wood boring Aculeates (Hym.).' Ent. Mon. Mag. 77: 241–4.

Artificial stumps constructed of a series of split blocks held together with wires. One or more holes are drilled into the blocks which may readily be interchanged or opened up for examination.

**Pickles, W. (1941).** 'Repairs to damaged nest-mounds by ants.' Ent. Mon. Mag. 77: 164–5.

In 20 days *Lasius flavus* brought up about 60 g. of soil in repairing damage to their nest-mounds. Building chiefly takes place on rainy days when the average weight of soil brought up was 10 g. per day.

**Pickles, W. (1941).** 'The variation in the *p*H of the soil of the mounds of the ant *Lasius flavus* F.' Ent. Mon. Mag. 77: 232–4.

Mounds increase in alkalinity with increase in depth as does the soil.

**Benson, R. B. (1941).** 'On some *Pontania* species, with a revision of the *proxima* and *herbaceae* groups (Hymenoptera Symphyta).' Proc. R. Ent. Soc. Lond. (B), 10: 131–6.

Various *Salix*-living species of this sawfly genus.

**Waloff, N. (1941).** 'The mechanisms of humidity reactions of terrestrial isopods.' J. Exp. Biol. 18: 115–35.

Woodlice keep themselves in moist air environments through moving about less rapidly as the R.H. increases and by making more frequent turns per unit distance travelled than they do in dry air.

**Ellis, A. E. (1941).** 'The Mollusca of a Norfolk Broad.' J. Conch. 21: 224–43.

An analysis of the habitat types and characteristic mollusc communities of Wheatfen Broad, Surlingham. The habitats form a drying-out series from open drainage ditches to oak-ash woodland. There are also artificial habitats such as raised banks and a garden.

(*d*) Small islands

**Harrison, J. W. Heslop (1941).** '*Hemaris tityus* taken in the Isle of Rhum.' Entomologist, 74: 210.

Recorded as swarming between 10 and 11 a.m., but some seen at 2 p.m. on one hot afternoon.

**Kevan, D. K. McE. (1941).** 'The insect fauna of the Isle of Eigg.' Entomologist, 74: 247–54.

Detailed list of insects and other terrestrial Arthropods.

## 2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

**Ministry of Agriculture and Fisheries (1941).** 'A farming type map of England and Wales. Explanatory text.' Second (temporary) edition, including black-and-white map on reduced scale only. The Land Utilization Survey of Britain. 16 pp. Price 2*s*.

The map, size 16·5 by 20 in., has dot-dash county boundaries, cross-hatched industrial patches, main towns, and black lines delimiting different farming types. (There were about 100 copies of a coloured map on scale of 10 miles per inch distributed before the rest were destroyed by enemy action, together with the printing plates.) The types shown are as follows: *Pasture types*: A. Predominantly dairying. B. Dairying supplemented by other enterprises. C. Grazing and dairying. D. Rearing, supplemented by several other livestock enterprises. E. Mainly rearing and sheep grazing. *Intermediate types*: F. Mixed farming with substantial dairying side. G. Mixed farming with substantial rearing or feeding side. H. General mixed farming. I. Corn, sheep, dairying. J. Farming based largely on wheat and cattle. K. Other intermediate types, with fruit, vegetables or hops. *Arable types*: Mixed farming based on arable production. M. Mainly corn and sheep farming. N. Corn and sheep farming, supplemented by cash crops. O. Mainly cash crop farming. P. Market gardening. Q. Other arable farming types. *Various*: X. Land of small agricultural value. Y. Marshes. Z. Varied farming on mixed soils, or unclassified. Distribution and reasons for each of these types are briefly categorized. The facts were collected before the present war.

**Stamp, L. Dudley and others (1941).** 'Fertility, productivity and classification of land in Britain. An explanatory bulletin to the land fertility map of Britain on the scale of ten miles to one inch (south sheet).' Land Utilization Survey of Britain. Temporary edition, with three black-and-white maps on scale of 20 miles to one inch. 36 pp. Price 3*s*.

Contains a useful summary of the available evidence, with county references, for classifying land, and of various organized surveys that have been done in recent years. The three maps represent good, medium and poor land types, distinguished by black-and-white hatched symbols superimposed on a mainly blank map showing county boundaries.

**Lowndes, A. G. (1941).** 'Rapid determination of water in animals and plants.' Nature, Lond. 148: 594–5.

Using an ordinary Soxhlet extractor with an outlet tap and the siphon tube blocked with mercury, the organism is placed in xylol and distilled at 135° C. As water is heavier than xylol, it separates out in the distillate and is readily determined.

**Holt, P. F. & Callow, H. J. (1941).** 'Rapid determination of water in animals and plants.' Nature, Lond. 148: 755–6.

A modification of the Dean and Stark method eliminates the inaccuracies caused by the adhesion of water droplets to the condenser column when solvents lighter than water are being used.

**Cockayne, E. A. & Darlow, H. M. (1941).** 'Wild hybrids of *Zygaena filipendulae*, L., × *Z. lonicerae*, Esp.' Ent. Rec. 53: 113–14.

Establishes, by genitalia preparations, the long-suspected occurrence of hybrids of the five- and six-spot burnet moths.

**Browne, F. Balfour- (1940).** 'British water beetles.' Vol. I, xx+375 pp., 5 pls., 89 figs. London (Ray Soc.). Price 25*s*.

The first part describes habits, structure and methods of collecting. Part 2, largely systematic, contains ecological notes. There are 72 maps of distribution by counties and vice-counties,

**Hinton, H. E. (1941).** 'The Lathridiidae of economic importance.' Bull. Ent. Res. 32: 191–247.

Keys and summaries of the distribution, habits, life histories and literature on this family of beetles.

**Blair, K. G. (1941).** '*Rhagium bifasciatum* Fab., and its varieties in Britain.' Proc. S. Lond. Ent. Nat. Hist. Soc. 1940–1: 39–42.

Key and plate of the colour variations of this common longicorn beetle.

**Thomas, I. & Jacob, F. H. (1941).** 'British Aphididae. I. The genus *Pentatrichopus* Börner (Hemiptera). Part I [–II].' Proc. R. Ent. Soc. Lond. (B), 10: 107–14 [115–23].

Keys and notes on host plants.

**China, W. E. (1941).** 'Systematic notes on the British species of *Corizus* auct. (Hem., Coreidae).' Ent. Mon. Mag. 77: 273–8.

Figures and keys for the identification of the British genera of Corizinae, Western European species of *Stictopleuras* and British species of *Rhopalus*. These are bugs.

**Hynes, H. B. N. (1941).** 'The taxonomy and ecology of the nymphs of British Plecoptera with notes on the adults and eggs.' Trans. R. Ent. Soc. Lond. 91: 459–557.

**Hynes, H. B. N. (1940).** 'A key to the British species of Plecoptera (stoneflies) with notes on their ecology.' Sci. Publ. Freshw. Biol. Ass. Brit. Emp. No. 2: 1–39.

The second of a series of illustrated pamphlets containing keys and references for identifying British fresh-water animals.

**Kimmins, D. E. (1941).** 'A new species of Nemouridae (Plecoptera).' J. Soc. Brit. Ent. 2: 89–93.

Includes figures of genitalia of *Protonemura montana* sp.n. and key to species of this genus.

**Kimmins, D. E. (1941).** 'A list of the Psocoptera of Kent, Surrey and Sussex, with a revised list of the British species.' J. Soc. Brit. Ent. 2: 93–8.

A valuable check-list of the 68 British species of Psocids, together with notes on recent changes in nomenclature, additions to the list, etc.

**Bagnall, R. S. (1941).** 'Notes on British Collembola.' Ent. Mon. Mag. 77: 217–26.

A systematic paper adding 12 species to the British list.

**Speyer, E. R. & Parr, W. J. (1941).** 'The external structure of some Thysanopterous larvae.' Trans. R. Ent. Soc. Lond. 91: 559–635.

**Scourfield, D. J. & Harding, J. P. (1941).** 'A key to the British species of freshwater Cladocera with notes on their ecology.' Sci. Publ. Freshw. Biol. Ass. Brit. Emp. No. 5: 1–50.

The contents are: foreword, introduction, keys, notes on ecology, references, diagrams.

### 3. PARASITES

**Benson, H. J. Craufurd- (1941).** 'The cattle lice of Great Britain. Part I. Biology with special reference to *Haematopinus eurysternus*.' Parasitology, 33: 331–42.

Records in detail the distribution of *Bricola bovis*, *Haematopinus eurysternus*, *Linognathus vituli* and *Solenopotes capillatus*, of which the first is the commonest. The incubation period for the eggs varied from 9 to 19 days. The average length of the instars of *Haematopinus eurysternus* is given and the complete life cycle took 28 days. Males lived on the host 10 days, females 16 days. None survived 96 hr. starvation. The maximum number of eggs laid was 24.

**O'Mahony, E. (1941).** 'Notes on Irish Siphonaptera: IV.' Ent. Mon. Mag. 77: 231.

Fleas from rabbit and hare, and from nests of puffin, Manx shearwater, skylark, kittiwake, herring gull and wheatear.

**O'Mahony, E. (1941).** 'Notes on Irish Siphonaptera: III.' Ent. Mon. Mag. 77: 208.

Fleas from nests of wheatear, great tit and house-sparrow.

**Thompson, G. B. (1940).** 'A list of the type-hosts of the Mallophaga and the lice described from them.' Ann. Mag. Nat. Hist. 6: 409–18.

**Thompson, G. B. (1940).** 'Notes on the Mallophaga of aquatic birds.—I. Mallophaga from divers (Gaviiformes).' Ann. Mag. Nat. Hist. 6: 513–22.

**Salt, G. (1941).** 'The effects of hosts upon their insect parasites.' Biol. Rev. 16: 239–64.

The species and individual type of the host frequently affects the size, rate of development and behaviour of insect parasites. It is therefore pointed out that for precise work on insect parasitology it is necessary to control and standardize the hosts.

**Beirne, B. P. (1941).** 'British species of Diplazonini (Bassini auctt.) with a study of the genital and postgenital abdominal sclerites in the male (Hym.: Ichneum.).' Trans. R. Ent. Soc. Lond. 91: 661–717.

They are all parasitic on the larvae of Syrphid Diptera, although they have been recorded as being bred from Lepidoptera and Coleoptera.

**Kimmins, D. E. (1941).** 'A swarm of ♂ Ichneumonidae.' Entomologist, 74: 214.

Large numbers of male *Cratichneumon annulator* running over turf on Coniston Old Man at 2600 ft.

**Whitehead, T. & Wood, C. A. (1941).** 'Aphid transmission of strawberry viruses.' Nature, Lond. 148: 597–8.

*Pentatrichopus fragariae* is the only British aphid known to be a vector of *Fragaria* viruses 1 and 2, though many other genera have been tested. Transmission by *P. tetrarhodus* has now been achieved, suggesting a specificity of relationship between the genus and strawberry viruses.

**Sproston, N. G. & Hartley, P. H. T. (1941).** 'The ecology of some parasitic Copepods of Gadoids and other fishes.' J. Mar. Biol. Ass. U.K. 25: 361–92.

Young whiting and pollack are infected by the blood-sucking adult female of *Lernaeocera branchialis* in shallow water. The older infected fish apparently linger inshore and in estuaries after the majority have migrated offshore. Factors influencing the distribution of the parasite and its effect on the behaviour of the host are discussed. No direct effect on the health or 'condition' of the fish could be detected. *Lernaeocera* probably spends not more than 2 weeks on its intermediate host—the flounder—and 6–8 weeks on the final—Gadoid—host. There may be five or six generations per annum which overlap. The lingering of the parasitized Gadoids results in an easy reinfection of the flounders. Similarly, sprats infected with adult female *Lernaeenicus* spp. linger inshore with the newly recruited estuarine stock of the following season. *Clavella uncinata*, a gill-parasite of Gadoids, has but a single host and appears to have no influence on the migration of the fish, though waters of lower salinity have a detrimental effect on this parasite. *Lepeophtheirus* spp. show a graded resistance to reduced salinity and those on flatfishes show the least, being strictly marine in occurrence.

**Sproston, N. G. & Hartley, P. H. T. (1941).** 'Observations on the bionomics and physiology of *Trebius caudatus* and *Lernaeocera branchialis* (Copepoda).' J. Mar. Biol. Ass. U.K. 25: 393–417.

*Trebius caudatus* is an ectoparasitic Caligid found chiefly on rays: records of its distribution on host species are given. It tends to collect near orifices on both surfaces of the fish where there

is the greatest mucus secretion. Older fish and those inhabiting deeper water are more often infected. The mean rate of infection from two localities near Plymouth was the same as that at Roscoff. An analysis is made of the complex gut movements connected with the dual function of feeding and intestinal respiration. *Trebius* uses as oxygen vector sea water entering via the anus, whereas *Lernaeocera* uses host blood. The evolution of the respiratory mechanism in parasitic Copepods is summarized.

## 4. FOOD AND FOOD HABITS

**Ware, A. Hibbert-** (**1940**). 'An investigation of the pellets of the common heron (*Ardea cinerea cinerea*).' Ibis, 4: 433–50.

Examination of 270 pellets showed percentage occurrence of mammals as follows: moles 55, water voles 27, and brown rat 9. Bird remains occurred in 18 pellets and a few showed reptile remains. Very few had remains of fish or Amphibia, but it is shown that the strong acidity of the heron's digestive secretions (pellets soaked in 100 ml. of water gave HCl concentrations from 0·6 to 1·82 g./l.) would leave practically no trace of this type of prey.

**Blair, R. H.** (**1941**). 'Nest-sanitation.' With additions from published sources by B. W. Tucker. Brit. Birds, 34: 206–15, 226–35, 250–5.

Considerable data about the methods employed by various species to keep nests clear of faeces, and the general forms of behaviour that ensure this. When the young are small the faeces are removed and swallowed by the parents; later the young assist by elevating their tails and the faeces are carried away; lastly the young evacuate the faeces over the side of the nest.

**Parmenter, L.** (**1941**). '*Bibio marci* L. (Dipt.) captured by garden warbler (*Sylvia borin* Bodd.).' Ent. Mon. Mag. 77: 153.

About six birds catching flies flying in the sunshine over the tops of 30–40 ft. oak trees.

**Worthington, E. B.** (**1941**). 'Perch in British lakes: a new fishing industry.' Nature, Lond. 148: 651–2.

Perch not only compete for food with trout but are at such a high density in Windermere that all are of small size. Wire-netting traps that are almost specific to perch have cropped about 46 lb. per acre from waters below 20 m. depth. This is providing a new source of canned fish and should improve the trout fishing.

**Carpenter, K. E.** (**1940**). 'The feeding of salmon parr in the Cheshire Dee.' Proc. Zool. Soc. Lond. A, 110: 81–96.

Results are given of an analysis of samples over a complete year. The average length of the fish used was 125 mm. The average volume of the food taken varied slightly, the highest amounts being found in February to April. Composition of the food is given in detail: sub-aerial prey is commonest in June and September, consisting principally of Hemiptera and Diptera. Benthic fauna occurs most frequently about July, and each group is found most abundantly at the time, when it would normally be available.

**Parmenter, L.** (**1941**). 'Further records of predacious flies and their prey.' Ent. Mon. Mag. 77: 154–5.

Includes records of Asilidae, Empididae, Muscidae and Cordyluridae.

**Wright, E. Barton-** (**1914**). 'Flour and the growth of *Tribolium*.' Nature, Lond. 148: 565–6.

Addition of either riboflavin or nicotinic acid to patent flour (35% extraction) greatly increases the growth of *Tribolium*. Experiments with various additions to a vitamin-free diet show that, although aneurin and vitamin $B_6$ are essential for pupation, there must also be present, even in patent flour, some other growth factor which is as important as any in the vitamin B complex. The factor occurs in liver and yeast.

**Hinton, H. E. & Stephens, F. L. (1941).** 'Notes on the biology and immature stages of *Cryptophagus acutangulus*, Gyll. (Col., Cryptophagidae).' Bull. Ent. Res. 32: 135–43.

This species of beetle will feed readily on a wide variety of fungi and will only rarely ingest other foods. It is capable of internal mechanical and external transmission of fungi. About 15% of the *Penicillium* conidia germinate after passing through the alimentary canal and these conidia have an enhanced germination rate.

**Kerr, J. G. (1941).** 'Unreaped harvest of the sea: the nutritive value of plankton.' Illus. London News, 5 July: 24.

After a short popular account of plankton, the author appeals for a committee to inquire into methods of locating concentrations of plankton, of separation from sea water and of preservation for marketing, as well as to inquire into the relative nutritive value of the different types.

**Cheng, C. (1941).** 'Ecological relations between the herring and the plankton off the north-east coast of England.' Hull. Bull. Mar. Ecol. 1: 239–54.

Plankton was collected by herring drifters using the Hardy Plankton Indicator (which has disk filters and is used with success commercially). The zooplankton was analysed in detail and comparisons made with the gut contents of herrings studied by Savage in the same area during the same three summers. Since the herring gill rakers are of approximately the same mesh as the nets used for plankton collection (60 to the inch), differences due to mechanical selection are probably slight or negligible. It is concluded that the herring selects the larger species of Copepods and, when these are scarce, feeds selectively on *Limacina* and *Sagitta*. Small Copepods are always relatively more abundant in the plankton than in the herring.

## 5. POPULATION STUDIES

**MacLagan, D. S. (1941).** 'Recent animal-population studies; and their significance in relation to socio-biological philosophy (Part I).' Proc. Univ. Durham Phil. Soc. 10: 310–31.

A useful revue of the main work on laboratory populations of Protozoa and insects.

**Ranson, R. M. (1941).** 'New laboratory animals from wild species: breeding a laboratory stock of hedgehogs (*Erinaceus europaeus* L.).' J. Hyg., Camb. 41: 131–8.

Although hedgehogs failed to breed in laboratory cages, 27 young were produced by five females in seven litters. Techniques are described for making the animals uncurl so that diagnosis of pregnancy can be made by palpation.

**Hammond, J. (1941).** 'Fertility in mammals and birds.' Biol. Rev. 16: 165–90.

Discusses the various factors affecting fertility in relation to the stage of the reproductive process at which they take effect: those influencing ovulation, fertilization and development of the fertilized egg respectively.

**Lack, D. (1940).** 'The behaviour of the robin. Population changes over four years.' Ibis, 4: 299–324.

Population changes over a period of three and a half years on about 20 acres of ground near Totnes, Devon. In this period 122 birds were marked. Many interesting results are given, though a warning is given against extracting too much information from small samples. Figures for length of stay (not survival, because it was not sure that birds, which ceased to be observed, had died) are as follows: males: up to the end of the study two had stayed at least three years, three had stayed two and a half years, four had stayed two years, and 19 had stayed less than two years; resident females: one had stayed at least three years, one had stayed two and a half years, two had stayed two years and one had stayed one year; migrant females: one appeared in three springs, four in two springs, and the rest appeared only once. The difference between the resident and migrant female populations is well brought out; of 32 observed 24 were migrants. Numerous other data are given on nestlings, which stayed in the area, the various matings which took place, the proportion of birds breeding, etc.

**Lack, D. (1941).** 'Notes on territory, fighting and display in the chaffinch.' Brit. Birds, 34: 216–19.

From observations on birds kept in an aviary it was possible to demonstrate that the presence of a dominant pair would entirely prevent any breeding behaviour in another pair.

**Perry, R. (1940).** 'Lundy: isle of puffins.' London (Lindsay Drummond), 267 pp., 37 photographs, 1 folding map. Price 12*s.* 6*d.*

The author spent five months in spring and summer of 1939 on Lundy Island, off west coast of Devon. Chief observations were on puffin, kittiwake, razorbill, guillemot. Total seabird breeding population (tables and map) in pairs was approximately 40,000 made up as follows: great black-backed gull 57; lesser black-backed gull 350; herring gull 3000; kittiwake 3000; guillemot 19,000; razorbill 10,500; puffin 3500; shag 110; cormorant 13; oystercatcher 23. Fulmars were present but not breeding. Estimate of 1000 breeding pairs of Manx shearwaters needs checking. Land-birds also counted; 22 species. Many notes on breeding behaviour of resident seabirds, migration on passage, and phenology.

**Moorhouse, S. (1940).** 'The heronries of an estuary.' Northw. Nat. 15: 225–8.

The recent history of four heronries in the vicinity of Morecambe Bay is described. The nests were counted in spring 1940 after the severe frost and snow and the numbers compared with previous years especially with those of the 1928 census. In three out of four the numbers had increased considerably. This may be connected with the pronounced decrease in numbers in other north Lancashire heronries in less secluded areas.

**Ticehurst, N. F. (1941).** 'The mute swan on the river Thames.' S. East. Nat. 46: 54–8.

Notes on the mute swan (*Cygnus olor*) on the Thames and other rivers, with details of ownership and illustrations of the marks used to identify the birds.

**Clapham, R. (1941).** 'The perch problem: a chance for reducing overpopulation in the Lakes.' Salm. Trout Mag. No. 102: 156–7.

Increase of perch in Malham Tarn, Yorkshire, and its effect on trout fisheries. Suggests that trapping would increase the national food supply as well as improve fisheries.

**Hutton, J. A. (1941).** 'Wye Salmon: results of scale reading.' Salm. Trout Mag. No. 102: 158–69.

The salmon fishery of the river Wye in 1940. The total catch of 3327 fish weighing 51,023 lb. was slightly below that of 1939 and well below the average of the last 30 years. The age composition of the stock showed a scarcity of large spring fish and of previously spawned fish.

**Went, A. E. J. (1940).** 'Salmon of the River Shannon.' J. Dep. Agric. Éire, 37: 254–310.

An analysis of the stock of 1928 and 1938 from scale readings. The construction of the hydroelectric scheme in 1928–9 altered conditions of access to the spawning grounds. In 1928 large spring fish formed 20% of the catch, grilse and small spring fish over 55%. The average age of a sample of smolts in 1938 was considerably higher (2·12 years) than in 1928 (1·98 years).

**Éire, Dep. Agric., Fish. Branch. [1941].** 'Statistics of salmon, sea trout and eels captured during each of the years 1939, 1937, 1935, 1933, 1931, 1929, 1927.' Pp. 1–19. (Government Publications Sale Office, 3–4 College St., Dublin. Price 6*d.*)

Gives number of fishing licences, weight and value of catches.

**Finney, D. J. (1941).** 'Wireworm populations and their effect on crops.' Ann. Appl. Biol. 28: 282–95.

A marked decrease in infestation from south to north of the country was shown to exist by the sampling determinations of wireworm populations on grassland intended for ploughing prior to cropping in 1940. Irregularity in distribution is seldom sufficient to render desirable differential cropping within fields.

**Lloyd, L. (1941).** 'Seasonal rhythm of a fly.' Nature, Lond. 147: 811–12.

Demonstrates a seasonal rhythm in the Chironomid *Spaniotoma minima* in sewage beds. A periodicity of emergence is shown, the interval between the peaks being less than that required for a complete life cycle. It is shown that a series of overlapping generations is running. This fly has no diapause and the presence of several flight periods a year will increase the chances of the adults finding the suitable still air for the mating flight.

**Lloyd, L. (1941).** 'The seasonal rhythm of a fly (*Spaniotoma minima*) and some theoretical considerations.' Trans. Roy. Soc. Trop. Med. Hyg. 35: 93–104.

From peaks in the curve of emergences and by applying the progress-temperature law, life cycles of successive generations can be traced, although there are several other generations emerging in between times.

**Buxton, P. A. (1941).** 'Studies on populations of head-lice (*Pediculus humanus capitis*: Anoplura). IV. The composition of populations.' Parasitology, 33: 224–42.

In about two-thirds of the 858 infestations examined there were 10 lice or less. Infestations over 100 never formed more than 10% of the infestations from one locality. In a single head the proportion of the sexes is often far from equal. In light infestations commonly all the adults are of one sex. When the density is unusually high, the proportion of males rises progressively. The mean number of larvae per female ranges between 5·4 and 10·9. There is a high mortality among the larvae, the death rate being higher in the third instar than in the other two.

**Haddow, A. J. (1941).** 'The influence of nutrition on egg-production and longevity in unmated female body-lice (*Pediculus humanus corporis*: Anoplura).' Parasitology, 33: 40–6.

Groups of ten lice were fed on man for 4, 8, 12, 16, 20 and 24 hr. per day. A pronounced and significant difference in longevity and egg-production rate was found between the 12 and 8 hr. groups, but below and above this level the differences were not significant.

**Benson, H. J. Craufurd- (1941).** 'The cattle lice of Great Britain. Part II. Lice populations.' Parasitology, 33: 343–58.

Study of seasonal variations in cattle lice populations and their distribution on the host at different times of year by monthly examinations of test cattle and a questionnaire to farmers. The regional distribution varies with seasonal variations of the whole population. Light intensity and seasonal fluctuations of the density of the animal's coat affect lice populations.

**Matheson, C. (1941).** 'The distribution of *Cimex lectularius* in towns in England and Wales.' Bull. Ent. Res. 32: 165–71.

Normally the degree of infestation increases with the magnitude of the town. Inland towns may have a lower degree of infestation than seaports.

**Pennington, W. (1941).** 'The control of the numbers of fresh-water phytoplankton by small invertebrate animals.' J. Ecol. 29: 204–11.

Experiments in beakers and tubs showed that the crustacean, *Daphnia pulex* and the rotifer, *Brachionus pala*, when in sufficient numbers, can reduce the numbers of phytoplankton very rapidly. This depletes the oxygen almost completely, the animals die, and the algae again increase. The same cycle occurs also in ponds, and at all times of year, though more slowly in winter.

**Gurney, R. (1940).** 'Some notes on the biology of the Copepod *Diaptomus castor*.' Ann. Mag. Nat. Hist. 6: 277–83.

Follows growth of a colony in a temporary pond at Cothill, Berks, from January until May, giving for each collecting date the number and percentage of individuals in various growth stages. The sex ratios of later stages are also given.

**Lucas, C. E. & Macnae, W. (1941).** 'Continuous plankton records: phytoplankton in the North Sea, 1938–39. Part I. Diatoms.' Hull Bull. Mar. Ecol. 2: 19–46.

The occurrence of patches of particular species or races and the movements of populations with water masses have been followed. The stability and persistence of other patches suggests continued suitability of conditions, due perhaps to a swirl or upwelling. Abundant production in these regions will probably affect the bottom fauna. Variations in diatom populations occurring in time and space were essentially similar to those found in the earlier survey. Crops in the southern area have, however, decreased since the 1935–7 period. There is possibly a correlation between this decline and the flow of water poor in phosphates from the English Channel into the southern North Sea.

**Rae, K. M. & Fraser, J. H. (1941).** 'Ecological investigations with the continuous plankton recorder: the Copepoda of the southern North Sea, 1932–37.' Hull Bull. Mar. Ecol. 1: 171–238.

Monthly samples taken with the continuous plankton recorder at a depth of 10 m. on four lines across the southern North Sea are analysed and possible errors discussed. The seasonal sequence of changes in the total Copepod population of different parts of the area was broadly similar from year to year. The intensity and extent of dense patches varied, being greatest in 1935 and 1937. These successful Copepod communities appeared just after dense and varied crops of spring diatoms. The importance of Copepods in food chains suggests that yearly fluctuations will be reflected in the general ecology of the region and will influence survival of young fish. Distributions of individual species are analysed. A group of four species was found to be responsible for most of the fluctuations. There were differences of detail and local patches of other species occurred, often repeatedly. The success of individual species varied from year to year.

**Kerr, J. G. (1941).** 'Oyster fisheries. Potentialities of Highland sea lochs.' The Scotsman, 18 June.

Oysters, formerly abundant in parts of Loch Sween, Argyle, have disappeared through smothering by fine mud. Artificial culture, after experimentation, is urged.

**Cole, H. A. (1941).** 'The fecundity of *Ostrea edulis*.' J. Mar. Biol. Ass. U.K. 25: 243–60.

Examination of oysters from various sources—native, tank-bred and relaid French—showed that the number of embryos is approximately doubled each year until the oyster is four years old, when it may be considered adult. The proportion of the population which matures in the female phase probably increases with age. For each year group the number of embryos is smaller later in the season and among the adults there appears to be a group of strong and a group of weak spawners, possibly the latter had passed through the male phase earlier in the season. The effect of current fishery practice on the local production of spawn is discussed.

## 6. MIGRATION, DISPERSAL AND INTRODUCTIONS

**Latter, O. H. (1941).** 'A factor in the dispersal of burdock (*Arctium Lappa*, Linn.).' Nature, Lond. 148: 726.

The fine yellow dust on top of a ripe burr is composed of very fine bristles which produce an irritation of the skin. It is suggested that this irritation may cause an animal with a burr attached to scratch it, and in so doing break it up and scatter the fruits.

**Worthington, E. B. (1941).** 'Rainbow trout in Britain: a survey prepared at the request of the National Association of Fishery Boards.' Pp. 1–64. Manchester. Also in Salm. Trout Mag. 1940, 100: 241–60; 1941, 101: 62–99.

The first North American rainbow trout were introduced into England in 1884. They have become established in Blagdon Reservoir (near Bristol), the Derbyshire Wye and other spring-fed, alkaline waters. In waters where they do not breed they are a useful fish for stocking purposes as over-population and dwarfing can be prevented. They are somewhat more tolerant than the native brown trout of warm, polluted or oxygen-deficient waters. The likelihood of the rainbow driving out the brown trout is not considered serious.

**Went, A. E. J. (1941).** 'Salmon Fishery Investment: a case where a good return has been realized.' Salm. Trout Mag. No. 102: 125–39.

Before 1851 the Ballisodare river system in County Sligo, western Ireland, contained no salmon, owing to impassable falls at the head of the tideway. Then fish passes were constructed and about 60,000 salmon eggs were put into the upper river. The undertaking was very successful; by 1878 the average catch of salmon was between 8000 and 9000 fish of an average weight of about 5 lb. and since then it has varied between 3000 and 6000 per year.

**Anon. (1941).** 'A clouded yellow butterfly invasion.' Nature, Lond. 148: 137.

*Colias croceus* from the Continent appeared in the first week in July in Lancashire, Cheshire and various other parts of north England. It is one of the spasmodic immigrations of insects, and there is no record of winter survival here.

**Cowley, J. (1941).** '*Sympetrum fonscolombii* Sélys (Odonata) in N. Devon and Somerset.' Entomologist, 74: 187.

**Dannreuther, T. (1941).** '*Sympetrum fonscolombii* in Devon and Hants.' Entomologist, 74: 187.

A very rare immigrant dragonfly. See also **F. C. Fraser, 1941,** ibid. 74: 240; **J. A. Riley, 1941,** ibid. 74: 264.

**Richards, A. W. (1941).** '*Sympetrum fonscolombii* (Selys) (Odon.) in N.E. Hants.' J. Soc. Brit. Ent. 2: 119.

Seven specimens of this rare migratory dragonfly seen. See also **F. J. Killington, 1941,** ibid. 2: 120.

**Morley, A. M. (1941).** '*Papilio machaon* in Kent.' Entomologist, 74: 152.

Records several adults, larvae and pupae of the swallow-tail butterfly from Kentish localities far from its fenland habitat.

**Fryer, J. C. F. (1941).** 'Time of flight of beetles of the genus *Agriotes*.' Ent. Mon. Mag. 77: 280.

A recent discussion on the wireworm problem brought out the lack of observation of the flight of the adult beetles. The author believes he has netted *A. obscurus, lineatus* and *sputator* at dusk.

**Andrews, H. W. (1941).** '*Paroxyna misella*, Lw., and *Oxyna parietina*, L. (Diptera: Trypetidae). A record of a failure and a success.' Proc. S. Lond. Ent. Nat. Hist. Soc. 1940–1: 36–8.

The first of these flies has been recorded as a pest of chrysanthemums recently introduced from Central Europe. The author collected it from *Artemisia vulgaris* (mugwort) in 1934, but was unable to find it in 1939. The larvae of the second were taken from mugwort stems in 1939 and the adults from growing mugwort plants in 1940.

**Waloff, Z. V. (1941).** 'The European migratory locust in the British Isles.' Bull. S.-E. Un. Sci. Socs. 76: [4–6].

Notes on the occurrence of *Locusta migratoria* and *Schistocerca gregaria* in Britain and the relation of occurrences to the appearance of swarms in Europe and North Africa.

**McMillan, N. F. (1941).** 'Molluscan fauna of Burton Marsh, Cheshire.' J. Conch. 21: 221–3.

Spread of *Hydrobia jenkinsi* from a fresh water cattle pond to slightly brackish gutters just above H.W.O.S.T. *Limnaea pereger* has also invaded the gutters, but has not spread so far as *Hydrobia jenkinsi*.

**Shrubsole, G. (1941).** '*Hydrobia jenkinsi* Smith on Beachy Head.' J. Conch. 21: 256.

Appearance of this species in large numbers in a foul cattle pond. It was absent from a cement trough where it was found the previous year.

## 7. REPORTS OF ORGANIZATIONS

**Dove Marine Laboratory, Cullercoats, Northumberland (1941).** Report for the year ending July 31st, 1940. Third series, No. 8, 16 pp. (Marine Laboratory Committee of King's College, Newcastle-upon-Tyne. Price 5*s*.)

Short reports are made of work on herrings, salmon, and pollution in the Tyne.

**Éire. Dep. Agric. Fish. Branch.** [**1941**]. 'Report on the sea and inland fisheries for the year 1939.' Dublin, 30 pp. Price 6*d*.

This report gives an account of the herring, mackerel, shellfish, salmon, sea trout and eel fisheries of Éire. Though largely concerned with administration, it includes statistical tables of landings, market returns and prices and brief notes on work in progress on the composition of herring shoals, fluctuations of the salmon fishery, the fauna and flora of rivers, pollution and artificial stocking with salmon and trout fry.